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A LIMNOLOGICAL INVESTIGATION OF THE PSAMMON
IN DOUGLAS LAKE, MICHIGAN, WITH ESPECIAL REF-
ERENCE TO SHOAL AND SHORELINE DYNAMICS¹

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This paper presents results of studies made at Douglas Lake, Michigan, to determine some limnological relationships of the psammolittoral zone. Recent investigations show that sandy shoals and beaches are not the biological deserts they have often been considered. Studies of the microbiology of fresh-water sandy shores began in 1926 when Sassuchin presented results of microscopic investigations of a beach of the Oka River, Russia. This work disclosed the presence of a varied assemblage of organisms in sand above water. In 1927, Sassuchin, Kabanov and Neiswestnova described details of the sandy beach environment with its algae, protozoans, rotifers, gastrotrichs, turbellarians, nematodes, tardigrades, oligochaetes, and dipterous larvae. They used the term "psammon" to designate this environment and assemblage of organisms and considered it, "analog dem Begriff 'Edaphon' France." Sassuchin (1930) gave an account of air-borne sands of the steppes of Kirghiz. This study was followed in 1931 by a paper dealing with conditions of life in water-accumulated sands of rivers and in shifting sands of deserts. Neiswestnowa-Shadina (1935) described faunal differences in sand from midstream to banks of the Oka River.

The most extensive European studies of the psammon were those of Wiszniewski (1937-'37) who presented papers dealing primarily with the rotifer fauna of sand on shallows and beaches of several Polish lakes and streams. His most detailed analysis of environmental conditions (1934a) concerned the beaches of Lake Wigry. Wiszniewski regarded the psammon as a special type of environment; whereas Sassuchin, *et al.* (1927) con-

¹ Contribution from the Biological Station and the Department of Zoology, University of Michigan.



sidered it as a transition between aquatic and soil habitats. Stangenberg (1934) made detailed chemical analyses of interstitial water from two beaches of Lake Wigry. Varga (1938) published a preliminary survey of the rotifers of the psammon of Lake Balaton, Hungary.

In the United States, Myers (1936) studied rotifers from the psammon of two New Jersey Lakes. Pennak (1939c, 1940) presented data concerning the physical and chemical environmental features of sandy beaches of certain Wisconsin lakes and described distributional features of rotifers, tardigrades, and copepods. Works closely related to psammon studies were those of Moore (1939), who investigated the microscopic benthic fauna of Douglas Lake, Michigan, and Moffet (1943), who made a study of a sandy, wave-swept shoal in Douglas Lake with regard to its dynamics and macrofauna. Copepods from sand interstices of oceanic beaches have been investigated by Wilson (1932, '35), Nicholls (1935), Otto (1936), Schulz (1937), and others. Some physical and chemical features of oceanic beach environments were described by Bruce (1928a, b).

Previous investigators of fresh-water psammon stressed organisms and environmental features of beach above water line, made little examination of conditions of life in submerged sand, and did not attempt to correlate features of the psammolittoral environment with shoreline and other lake processes. In the present study, environmental analyses of the psammon were made and correlated whenever possible with some phase of shoreline and shoal dynamics.

The writer is indebted to Paul S. Welch, under whose direction this investigation was conducted; to M. V. Denny, University of Michigan, for mineralogical analyses of sands and assistance in determining products of oxidation of sulfides; to Ruth Patrick, Academy of Natural Sciences of Philadelphia, for assistance with diatom identifications; to W. T. Edmondson, Harvard University, for rotifer identifications; and to G. W. Prescott, Michigan State College, for identifications of algae other than diatoms.

REGION STUDIED

Wiszniewski (1933) proposed the term *psammolittoral* to distinguish that sandy zone extending from an unspecified region in a lake to a distance of a few meters above the water line. He divided the psammolittoral into three parts: "hydropsammon" ("renferme les microorganismes vivant dans les sables constamment immergés"); "hygropsammon" ("embrasse l'ensemble de microorganismes liés à la surface des parties exondées de la plage, qui s'étendent immédiatement au-dessus de la limite de l'eau jusqu'à un metre environ"); and, "eupsammon" ("renferme les organismes vivant dans parties plus extremes de plage, à partir d'un metre environ"). Thus the hygropsammon corresponds roughly to the inner beach, and the eupsammon to the middle beach (Welch, 1935, Silvey, 1936).

In the present investigation, the psammolittoral zone is considered to include sandy beaches and shoals from 2-6 meters above water line to that region in the lake where sandy bottoms become overlaid with other materials. Thus included are the supralittoral, eulittoral, and littoral zones of Nauman (1928) and of Lenz (1928). In Douglas Lake the lakeward bound-

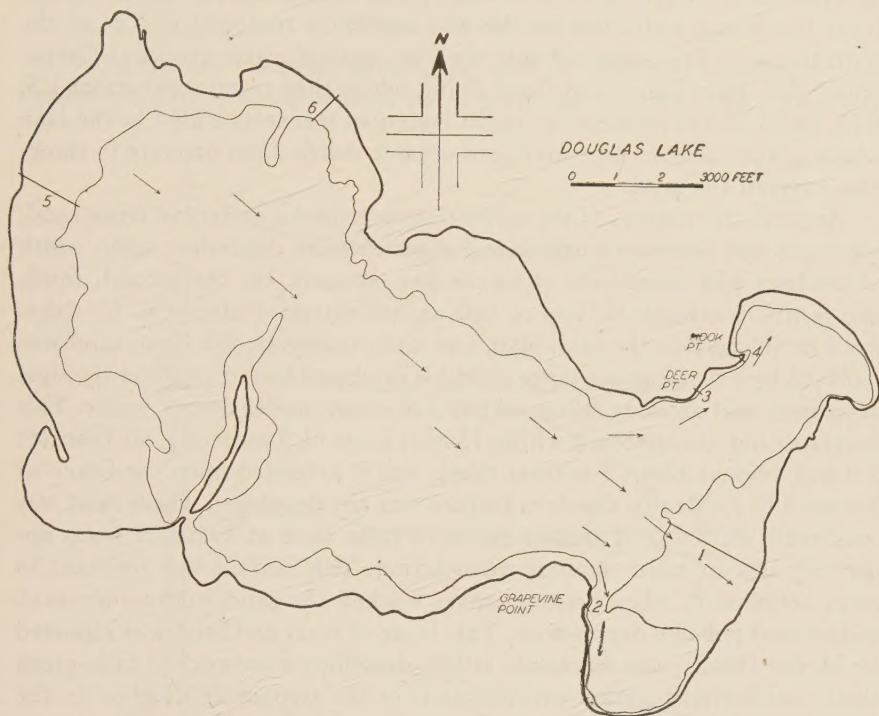


FIG. 1. Outline map of Douglas Lake, Michigan, showing 5 foot contour and locations of 6 sampling transects. Arrows indicate paths of water movements due to northwest winds.

ary of the psammon closely parallels the five foot contour shown in Figure 1.

In Figure 1 are shown 6 sampling transects in Douglas Lake, each of which extends from upper to lower limits of the psammolittoral zone. Distance so included varies on different transects. Sampling stations on each transect were closely spaced near water line (0.2-0.5m.) and at intervals of 10, 20, and 50 m out on wider shoals. Stations upon each transect were numbered with reference to the water line. The waterline was designated as the zero (O) position and stations above and below were listed as distance in m from the water line. In order to avoid confusion of shoal and beach stations, stations below water line are preceded by a minus sign

(—). It is believed that the six locations selected for transects offered sufficient diversity of conditions to permit evaluation of some major factors affecting the psammon.

The greater part of the Douglas Lake psammolittoral zone is included in the hydropsammon. Lakeward extensions of transects varied from 7 m at Transect 2 to 750 m at Transect 1; and shoreward extensions varied from 2 m above water line on the first and third transects to 6 m at the sixth transect. Transects ended under 2 m depth of water except at Grapevine Point, Deer Point, and Hook Point, where they terminated under 1.5, 1.75, and 1.25 m respectively. In all instances transects ended in the lake where a layer of flocculent marl and organic debris 1 cm or more in thickness covered the sand.

Areas in the vicinity of the water line presented a surface of clean sand, lakeward and shoreward extensions of which were dependent upon width of shallows and magnitude of waves and currents. On the second, third, and fourth transects, bottom of this nature extended almost to the lakeward limits; but on the first, fifth, and sixth transects, the clean sand was replaced by a firm surface layer in which sand was bound together by algal deposited marl on more lakeward parts of shoals under deeper water. This firm layer did not approach within 75 m of shore on Transect 1, on Transect 5 it was evident about 7 m from shore, and it extended upon the beach at Transect 6. Evidently this firm surface was not developed where sand was constantly shifted; and greater extent of clean sand at Transect 1 was apparently due to more vigorous wave action. This surface was resistant to wave action and, when broken, waves washed the sand from underneath and formed pot-like depressions. This layer of marl and sand was reported by Moffet (1943); and Sassuchin (1930) described a network of blue-green algae that bound together surface sands of the steppes of Kirghiz. In the vicinity of Transect 6, where no wave action was observed, greater quantities of marl were incorporated in the sand.

The psammon at Douglas Lake supports very few rooted plants, and those present are chiefly scattered bulrushes and short pondweeds. The second, third, and fourth transects ended at plant beds near shore, and plants were not present along those transects. The three other transects passed through scattered bulrushes and *Potamogeton* spp. that occurred on wider shoals. The sun shone upon beach sections of the first and second transects only during the afternoon, and the beach section of Transect 4 was shaded throughout the day. Beaches of the third, fifth, and sixth transects were never shaded; and shoals of all six transects were exposed to rays of the sun. Other than that incorporated in the firm surface layer described above, very little marl was present at depths sampled on shoals. Marl deposits in the form of narrow windrows about 1 m above water line were observed at Transects 2 and 4.

Collections and field observations were made during the summers of 1940, 1941, and 1942. During the first two summers a few exploratory samples were taken from shoals and beaches of other lakes; but in 1942 all work was confined to six transects in Douglas Lake.

METHODS OF STUDY

PHYSICAL FEATURES

Temperature readings were made with a corrected laboratory thermometer. Temperature in sand was determined at a depth of 2.5 cm with

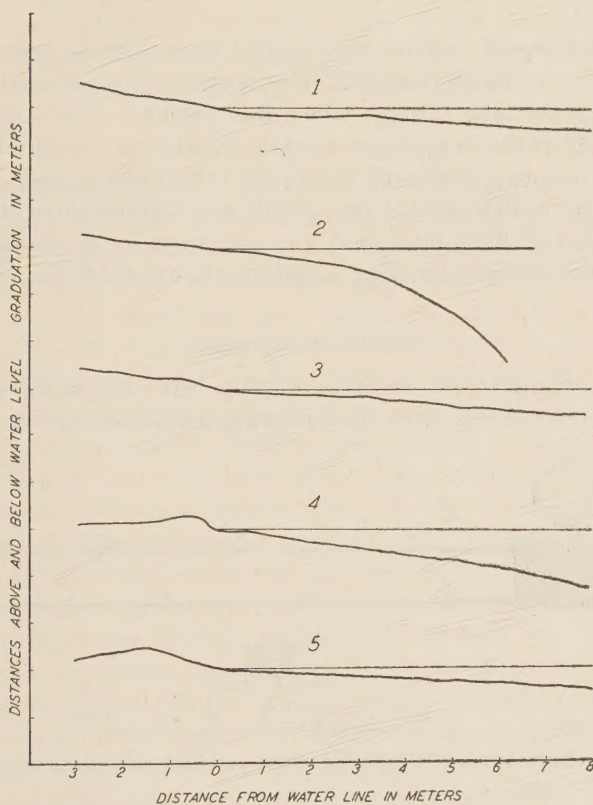


FIG. 2. Profiles of water line regions of the first five transects.

the thermometer *in situ*. Lake and air temperatures were measured 1 cm above the sand.

Grade analyses of sand were made by shaking dried samples through a series of Tyler Standard Screens of 4.699 mm, 2.362 mm, 1.168 mm, 0.417 mm, 0.208 mm, and 0.147 mm mesh sizes. Samples were obtained as

cores by use of brass tubes having an internal cross-sectional area of 10 sq cm. Each core served as a single sample, or, when cores were cut into lengths of 1 cm, as a vertical series of samples. Brass tubes were thrust vertically into the sand, the upper ends were then corked, and tubes were removed and lower ends corked.

Wave and current data are based upon observations that were made with the aid of weighed corks and *Scirpus* spp. culm sections. Segments of *Scirpus* culms are satisfactory indicators since they float low in the water; and many indicators are available from a single culm. Direction, velocity, duration, magnitude, frequency, and effects of currents and waves were recorded.

Interstitial organic matter was washed from sand by placing a 10 cc sample in 32 cc of water contained in an evaporating dish and by stirring sand with a glass tube through which was passed a slow stream of compressed air. After the sample was washed and stirred 3 minutes, the water was poured into two graduated centrifuge tubes; and organic matter was measured after centrifuging. Each sample was washed three times.

Penetration of light into sand was measured by a photoelectric cell apparatus constructed according to specifications of Atkins, Clarke, *et al*, (1938).

CHEMICAL FEATURES

Samples of interstitial water were taken with the water sampler described by Irwin (1942) with the following modifications: A small brass

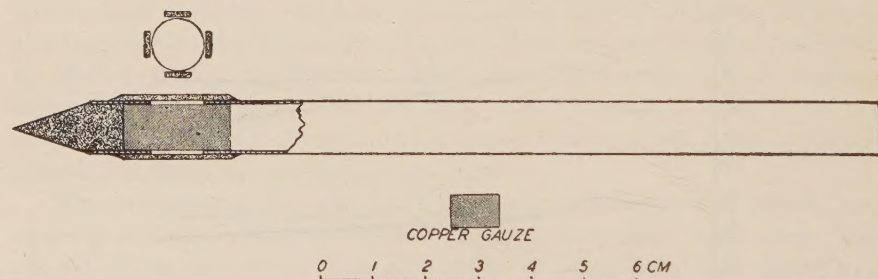


FIG. 3. Details of water sampler tube. Copper gauze and brass side braces are soldered to the brass tube.

sampling tube with rounded spear point and gauze-covered intake ports (Fig. 3) was attached to the intake hose; and suction through the sampler was brought about by flow of water from an evacuation chamber devised by use of a brass core-sampler tube, the upper end of which was attached to the suction hose of the sampler by means of a one-hole stopper and glass tube. The lower end of the evacuation tube was supplied with another one-hole stopper and glass tube to which was fastened a short length of

rubber tubing. A screw clamp placed on this tubing permitted regulation of flow from the evacuation tube. To prevent backflow, clamps were placed on the intake hose and on the hose between the two bottles immediately after the larger bottle was filled. Water was withdrawn from sand at a depth of 4 cm with intake ports of the sampling tube in either a horizontal or slanting position. Withdrawing water at this depth gave greater assurance of obtaining an uncontaminated sample. When the larger bottle was filled, the smaller bottle had overflowed six times, and its final 40 cc were used in tests for dissolved oxygen. Tests for free and half-bound carbon dioxide, hydrogen ion concentration, and phenolphthalein alkalinity were made from the contents of the larger bottle. Water analyses were made according to Standard Methods for the Examination of Water and Sewage (8th. ed., 1936). Dissolved oxygen procedure was modified as described by Irwin (1942).

BIOLOGICAL FEATURES

Sand samples for study of organisms were also taken with brass tubes. When samples were taken from the shoal, lake water was removed from the tube with a pipette after the lower end was capped. Each core served as a vertical series of samples. Cores were pushed to tops of tubes by use of a plunger that closely fitted their inner walls; and successive 1 centimeter-lengths were cut off with a spatula. Each 1 cm length of core provided a 10 cc sample. Sections of core to a depth of 6 cm were treated in the following manner: Each segment was placed in a 16 cc screw-cap jar containing 4 cc of a saturated solution of menthol, which served to relax the animals. Later examination showed that the menthol was efficient for sand samples whose interstitial volume contained some air, but it was not often satisfactory for sand from lower beach or shoal. After 10 minutes the jar was filled with a solution of glycerine (40 per cent) in 4 per cent formalin.

Organisms were washed from sand by the method described for the separation of sand and organic matter. Each sample was washed three times and the organisms concentrated by centrifuging the wash water. Organisms were returned to the original sample jar which was then filled to 16 cc with water. Other methods of separation, such as shaking sand with a small volume of water in a large bottle, were tried; however, the method outlined above gave greater numbers of psammo-organisms.

For counts, the contents of the sample jar were agitated, 1 cc removed and placed in a 1 cc Sedgwick-Rafter counting cell. Washing of sand resulted in a mixture of organisms and interstitial organic debris in the wash water. In many instances the amount of debris was too small to interfere with counting. When quantities of organic matter were too large to permit an accurate enumeration of organisms contained in 1 cc taken directly from the sample jar, 1 cc was diluted to 4 cc with tap water, and counts were made from 1 cc of the diluted sample. Greater dilution induced inac-

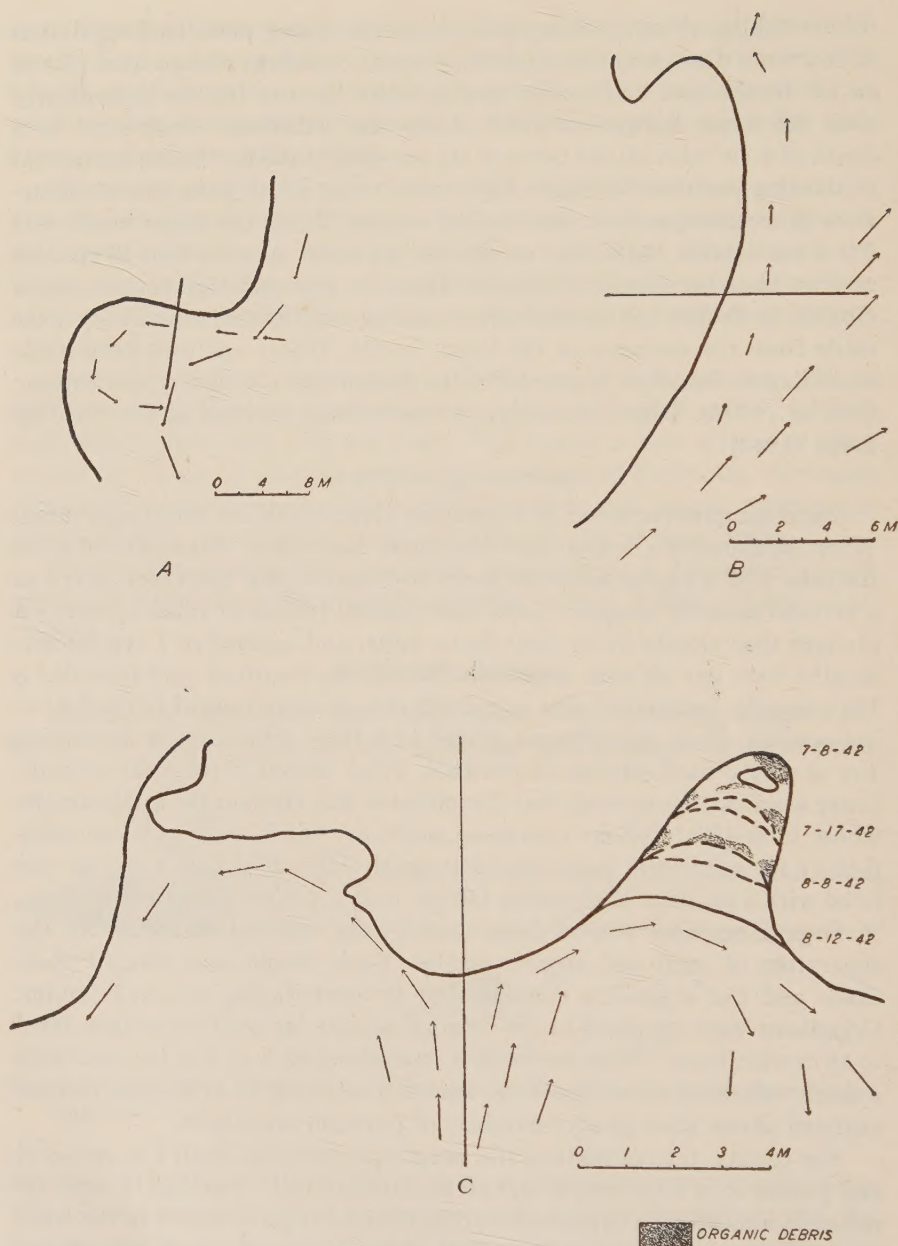


FIG. 4. Shoreline details and current paths at Transects 2, 4, and 5. Positions of transects are shown by solid ruled lines. A. Transect 2. Long arrows indicate currents due to northwest winds and short arrows show paths of currents caused by east winds. B. Transect 4. C. Transect 5. Time consumed in the filling of the small bay is shown by dates opposite the various shorelines. Broken lines show intermediate stages in filling, and solid lines indicate original and final shorelines.

curacy; and since dilution of this degree did not sufficiently disperse organic matter to permit counts of samples from Transect 6, a method was devised to separate debris from the majority of organisms. In this method, 1 cc of sample containing debris and organisms was permitted to flow slowly from a large-bore pipette onto the surface of a 13 per cent solution of glycerine contained in a separatory funnel. Most organisms settled to the bottom in 10–15 minutes and the organic debris remained near the surface. Organisms were then separated from debris by opening and closing the stop-cock. The most suitable strength of glycerine solution was determined by experimentation. It was necessary to place the sample upon the surface of the glycerine with as little disturbance of the latter as possible. This method was well adapted for separation of diatoms, most green algae, rotifers, oligochaetes, nematodes, and gastrotrichs, but permitted many blue-green algae (Chroococcaceae) to remain with the debris. Since this method was the best devised, counts of Chroococcaceae for Transect 6 were adjudged to be only approximate. Organisms were examined and counted under a compound microscope fitted with a Whipple ocular counter at a magnification of 100 diameters. Counts were made for the entire cell with the exception of diatoms whose average number per cu mm was obtained by averaging counts of 10 cu mm. Numbers of all forms were converted into number per cc of sand by averaging counts of 2 separate 1 cc lots from the 16 cc contained in the sample jar.

Lake plankton was collected with a Kemmerer sampler and a standard plankton net of number 20 bolting silk. Organisms contained in 12 l of lake water were concentrated to 16 cc and preserved with formalin and glycerine. Counts of psammo-organisms contained in the plankton were made of two 1 cc samples from each concentrate. Three thousand six hundred sand samples and 420 plankton samples were examined.

PHYSICAL FEATURES

TEMPERATURE

The thermal picture of shoal sand appeared to be affected by two factors, viz., insolation and lake temperature. In shallow regions (25 cm depth or less) the sand was warmer than the water above it during periods of calm and direct insolation. This heat was readily lost to the lake when the latter cooled. In early morning sand of the shallows was usually cooler than the overlying water. Sand under deeper water (50 cm depth or more) was found to be slightly below lake temperature at all times. Deeper regions of the shoals apparently owed their heat to the lake alone, since they were never observed to be warmer, and they contributed heat back to the water above as it cooled. Shallow regions, often warmed directly by the sun, contribute to as well as help maintain lake temperature. Wave action interferes with insolation of sand under water.

Beach thermal relations have been studied by Sassuchin, *et al.* (1927),

Wiszniewski (1943a), and Pennak (1940). The most detailed descriptions are those of Wiszniewski. He considered insolation and evaporation of interstitial water the two most important factors; but, inasmuch as the effects of these two agencies are modified by meteorological conditions, he thought the latter should be considered primary determinants of beach temperature. Since heat data obtained on beaches in this investigation support that of previous investigators reference may be made to their papers for details concerning this feature.

GRADE DISTRIBUTION OF SAND

Average percentages of different grades of sand upon each transect studied are shown in Table 1. Material retained by screens of 4.699, 2.363,

TABLE 1. Average percentages of different grades of sand. Values in body of table are percentages of sand retained by screens of mesh sizes indicated by column headings

Transect	4.699 mm.	2.362 mm.	1.168 mm.	0.417 mm.	0.208 mm.	0.147 mm.	Through 0.147 mm.
1	5.96	0.79	0.44	24.13	62.25	4.32	1.93
2	0.0	0.01	1.26	42.16	56.54	0.17	0.78
3	29.24	1.49	1.01	15.35	47.81	4.28	0.75
4	0.14	0.22	0.61	42.88	54.61	1.48	0.29
5	9.95	2.35	2.03	22.90	58.81	3.03	0.92
Average all transects	9.06	0.97	1.07	29.48	56.00	2.65	0.78

and 1.168 mm meshes is classified as gravel, that retained by 0.417 mm mesh as coarse sand, that retained by 0.208 mm mesh as medium sand, and that passing 0.208 and 0.147 meshes as fine sand.

Curves representing grade patterns of sand in terms of percentage of fine sand at each station to depths of 1 and 6 cm are shown in Figure 5. For this purpose, sand retained by mesh sizes of 0.417 mm or larger was arbitrarily classed as coarse, and all that passed 0.417 mm mesh as fine. The figure discloses considerable variation in distribution of fine grains along the five transects as well as differences in surface sand and that to depths of 6 cm. Inasmuch as the first cm is most readily affected by waves and currents its grade arrangement may not correctly represent major influences involved in selectivity of sand transportation. However, movements of the top layer are not without significance to psammo-organisms. Analysis of effects of waves and currents upon grade distribution of sand is reserved for sections dealing with those factors.

Grade and Pore Space

Previous workers (Sassuchin, *et al.* 1927, Bruce, 1928a, Wiszniewski, 1934a, and Pennak, 1940) have investigated the relationships of sand grade

to pore or interstitial space. Since, with few exceptions, they all report similar conclusions, and since no additional or conflicting data were obtained by repeating their experiments in this investigation, the reader is referred to their papers for detailed information upon this feature. Inter-

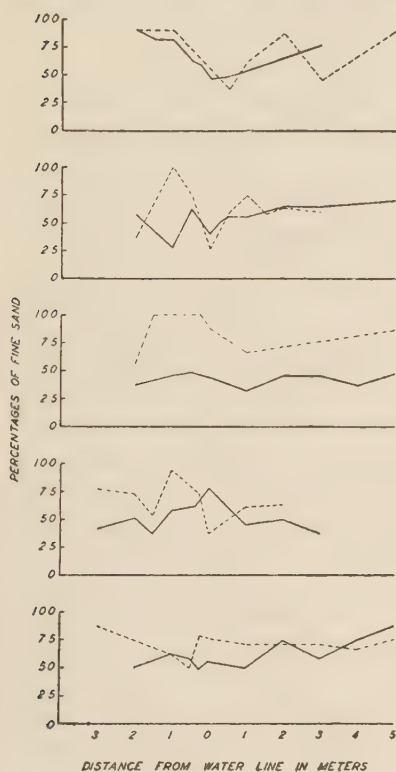


FIG. 5. Grade distribution of sand (in percentages of fine sand) upon the first five transects. Solid lines represent sand to a depth of 6 cm and broken lines indicate sand to a depth of 1 cm. Landward ends of transects are to the left.

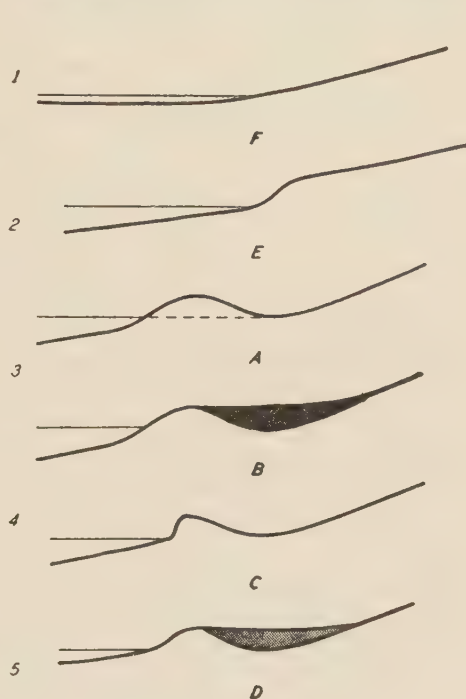


FIG. 6. Influences of water movements upon beach and shoal profiles. A. Sand ridge formed just before water line. B. Ridge back-filled with sand. C. Ridge partly removed by alongshore current. D. Back-filling of a partly removed sand ridge. E. Slope of beach and shoal resulting from alongshore currents. F. Slope of beach and shoal due to heavy waves.

stitial space as measured by retention of greater volumes of water has been shown by Bruce to become larger with increasing fineness of graded marine beach sands. Pennak found grades of lake beach sand from 1.17 to 0.21 mm grain diameter to be fairly uniform in percentage pore space—roughly around 40 per cent. Graded sand from Douglas Lake beaches was found to exhibit a slight increase in pore space in finer grades, but all sizes comparable to those reported by Pennak averaged around 40 per cent interstitial

volume. Ungraded sand from the first five transects varied from 37 to 41 per cent interstitial volume. In view of the approximation nature of the method devised by Bruce (1928a) these figures cannot be said to differ significantly from those of 37, 42, and 39 per cent pore space in ungraded sand reported respectively by Sassuchin, *et al*, Wiszniewski, and Pennak.

Grade and Capillarity

Excepting that added by waves and rain, interstitial beach water results from capillary rise of water from the lake or from water tables. Thus, in some respects, per cent saturation of a beach is affected by factors influencing capillarity. After testing rate of capillarity in different grades of sand, Bruce (1928a) concluded that rate of capillarity is a function of grade, or, "... more strictly, of the width of the capillary channels between the grains, since this, irrespective of the total volume of the pore space, becomes less as the grains decrease in size." Tests of rate of capillarity in graded sands made by Bruce, by Pennak (1940), and during the course of the present study show a more rapid and greater rise of water in finer grades. However, Bruce found that ungraded sand from an oceanic beach possessed a higher rate of capillarity than any of its constituent grades. Pennak noted that only the finest grades from lake beaches (0.21 mm or less grain diameter) possessed a higher rate of capillarity than ungraded sand. Results of capillarity tests made with graded and ungraded sands at Douglas Lake closely paralleled those of Pennak. Rise of water in dried ungraded sands from each of the first five transects in glass tubes 1 sq cm in internal cross-sectional area varied from 86 to 89 mm in 24 hours. In the finest grade (grains less than 0.147 mm in diameter) water rose 163 mm in the same period of time. High rate of capillarity in ungraded sands is due to filling of pore space between larger grains by smaller grains which results in smaller capillary spaces than those that occur in all but the finest of grades.

Continued movement of capillary water up through a beach is induced by evaporation of interstitial water from the surface. Rate of evaporation is affected by meteorological conditions, but evaporation is at approximately the same rate from sand of all grades (Bruce, 1928a).

Inasmuch as ungraded beach sand had approximately the same per cent pore space as any of its constituent grades, and since there were but slight differences in rate of capillarity in ungraded sands, it may be safely assumed that grade was in itself of minor importance in determination of landward extent of the psammon on any one of the first five Douglas Lake transects. A more important factor governing amounts of surface water in a beach would appear to be height above water level as expressed in slope. Reference to profiles (Fig. 2) and extent of capillary rise of water given above should serve to indicate limiting influences of greater angle of slope.

SLOPE OF BEACH AND SHOAL

Profiles of the first five transects are shown in Figure 2. Greater degree of slope limits both lakeward and shoreward extensions of the psammolittoral zone. In the lake, greater depth of water results in deposit of other material upon the sand nearer shore; and upon the beach, increased height above water level reduces quantities of water in surface sand nearer the lake. Profiles are altered by waves and currents and by fluctuations in water level as will be described below.

WAVE ACTION AND CURRENTS

Nature of Wave Action

Consideration of the physical features involved in waves and currents is properly beyond the scope of a biological paper. However, movements of sand and other materials of importance to psammo-organisms are largely dependent upon waves and currents; and some discussion of their

TABLE 2. Calculated maximum onshore height; and nature of wave actions observed at each transect

Transect	Calculated maximum onshore height (Hawksley)	Direction most frequent wave action	Degree most frequent wave action	Direction other observed wave actions	Degree other observed wave actions
1	3.49 ft.	onshore	heavy	oblique alongshore	moderate
2	1.5 ft.	onshore	moderate	alongshore	light
3	1.3 ft.	alongshore	moderate	oblique alongshore	moderate
4	1.3 ft.	oblique	light	onshore	light
5	3.49 ft.	onshore	moderate	alongshore	light
6	No wave action observed				

role in this respect cannot be avoided here. The subject of waves and wave actions has a voluminous literature (Johnson, 1919) and the following account is concerned only with those features which are of significance to the psammon. For enumeration and description of factors involved in production and in various effects of waves, reference may be made to Cornish (1910, 1914, 1934), Johnson (1919), and Stevenson (1886).

Height of waves is largely dependent upon velocity of wind and distance of open water or fetch across which the wind blows. Maximum height of waves in Douglas Lake (across longest fetch of 3.19 nautical miles, and which could be attained at Transects 1 and 5) is 2.68 ft when calculated by the formula of Stevenson (1886) and 3.49 ft when calculated by Hawksley's formula (quoted by Whipple, Fair and Whipple, 1927). Since a modification of Stevenson's formula is considered necessary for short distances, the latter figure is probably more correct. Features of wave action upon shore in the vicinity of each transect are given in Table 2. It must be

emphasized that the formula of Hawksley depends upon maximum winds; and waves of near calculated height were not observed at all transects.

Water deposited upon a beach by waves breaking directly onshore returns to the lake through and over the surface of the sand. Returning surface water meets new waves and cushions the shore from the shock of their impact. A zone of "confusion" (Johnson, 1919) is produced where waves fall upon returning water, and wave energy is largely dissipated. The crest of the wave, which falls first, augments the quantity of water moving lakeward and sends some of its own water upshore. The remainder of the breaking wave, which contains more water, apparently checks lakeward movement of water and adds much volume to the water moving up the beach, giving it added momentum. Water thus moved to upper regions of the psammon may flow directly back and become involved with later waves, or it may find a depression and flow off to one side. Much of it sinks into the sand in either case. Under conditions of direct onshore waves breaking upon a smooth strand, movements of this water have more effect upon the shore than the waves responsible for it (Johnson, 1919). Water pushed up by waves plays an important role in water supply of the eupsammon. Return flow to lake through sand of middle and lower beach was stronger than suction induced by the water sampler. Waves striking a bank obliquely were not observed to affect the upper regions; and along-shore waves evidently affected only the lowest area of a beach.

Currents Induced by Wave Action

Water returning down beach during periods of direct onshore wave action, although checked momentarily by each oncoming wave, eventually flows on down the shoal and forms a current (undertow) along the bottom. Indicators well suited to observation of undertow were found to be water-logged dead leaves that waves often disinterred from shoal sand. Such leaves move readily in the weak current but remain near the bottom. As each oncoming wave passes, the leaves rise and then drop and move out. Undertow varied in velocity from 4 ft per minute near shore to 12 ft per minute 25 m offshore.

Several small coves were observed to possess both onshore and offshore surface flow during periods of direct onshore wave action. As shown in Figure 4c, the small bay that led into Transect 5 was observed to have three surface currents at times of onshore waves. Here rate of incoming and outgoing flow was 20 ft per minute. Sand ripples were formed under offshore currents, but sand under the onshore current was smooth. Along-shore waves and those striking shore obliquely were observed to initiate alongshore currents that varied in duration with intensity of wave action. Small oblique tongues of sand were sometimes formed by shore drift.

Alongshore flow with velocity of 0.03—8 ft per second was observed

between Transects 3 and 4. At Hook Point currents swung around the bend of the hook as shown in Figure 4b. They slowed past the bend and most of them moved across the transect oblique to shore. Weaker currents sometimes flowed parallel to shore with some divergence toward shore. Velocity decreased from 0.3 to 0.2 and from 0.5 to 0.3 ft per second as moving water neared the shoreline. The weakest current noted near shore had a velocity of 0.1 ft per second. Flow was also observed to slow over deeper water farther offshore and it usually died out a little beyond the point of the hook. Alongshore currents paralleled the water line at Transect 3 and varied from 0.3 to 8 ft per second.

Currents due to northwest winds coursed past Transect 2 in the manner indicated by large arrows in Fig. 4a; whereas, currents due to winds from the east paralleled the shore as shown by small arrows. Flow of greater velocity (resulting from northwest winds) drew slightly away from shore and persisted for some distance down the west side of the bay; and weaker currents due to east winds usually stopped near the center of the cove.

Effects of Waves and Currents

Slope of Beach and Position of Water Line

On beaches mainly subjected to onshore wave action, slope from beach to shoal was uniform as shown in Fig. 6f; and transects most affected by alongshore wave and current actions had a steep bank just above water line as shown in Fig. 6e. Either type of profile could be altered by change in direction of water movements. Although sand cut by alongshore currents returned to uniform slope when subjected to strong onshore waves, and although beaches with uniform slope were cut by alongshore currents, profiles of beaches and shoals usually indicated the direction of prevailing wave and current actions.

Psammon profiles are also altered by beach building—a process usually attributed to onshore waves. Sand is added to the water line in the form of a ridge that exhibits a profile, as shown in Fig. 6a, which slopes uniformly from a high point between old and new water lines to low points at each. Newly deposited beach is often cut by alongshore currents until it has a sharp lakeward face (Fig. 6c), is removed entirely, or loses its identity when the low landward space is filled with sand (Fig. 6b). Observations indicate that ridges of this sort are more commonly formed by waves of moderate power, and sand deposited in them is apparently carried to shallows from deeper shoals. Since grade distribution of sand on newly formed ridges shows a greater percentage of finer grades on summits and lesser percentages at old and new water lines, evidently the finer grades of sand are involved in the formation of such structures. Ridges formed by moder-

ate waves are often obliterated by waves of greater power, and beach and shoal return to uniform slope.

Because of little resistance to waves and currents, most beach ridges do not persist for longer than a few days. Many that remain are incorporated into permanent beach when shoreward low areas become filled with sand. Some were observed to persist in unaltered form when fall in lake level removed them from the area affected by water movements. According to Moffet (1943), moderate waves add material of ridges to middle beach, and heavy waves push this elevation back to form a permanent part of the outer beach. On shallow shoals ridges are often formed short distances offshore, and such sandbars have the same profile and grade distribution of sand that characterize beach ridges. Bars are usually small and, unless protected by small bays, ephemeral. Bars formed by waves are often instrumental in filling small coves with sand and so rounding out shoreline as shown in Fig. 4c. Currents also deposit sand at water line; and, although such deposits are usually in the shape of spits, ridges similar to those formed by onshore waves result when currents slow and swirl out near shore.

Ridge formation results in much altered profile of beach and shoal. However, it is the tendency of waves and currents to maintain a smoothly sloping beach and shoal; and additions to shallows and beaches in the form of ridges or spits are soon removed or so altered as to bring about a smooth slope. Stages in processes of ironing out ridges are shown in Figure 6.

Grade Distribution of Sand

The variations found in grade distribution of sand on the first five transects were believed to be due primarily to differences in intensity and direction of prevailing wave and current actions. Water in motion exerts a selectivity in transportation of various grades of sand that is roughly proportional to the magnitude of the movement. Finer grades are probably affected by all movements of water, whereas coarser grains are moved only by stronger waves or currents. Ungraded sand subjected to frequent water movements should be graded to some extent, with coarser grades remaining near their original position and finer grains being distributed according to size along the path of water movement. Since direct onshore action results in flow of water in two directions from the shoreline, a sorting should be evident in which finer sands are moved above and below water line and coarser grades left in the immediate vicinity of the water's edge.

Selectivity of this sort was evident at Transect 1 (Fig. 5), where prevailing wave action was directly onshore, to a depth of 6 cm. Grade pattern of surface sand (to a depth of 1 cm) did not conform to this arrangement; but it may or may not have represented prevailing wave action, and

surface sand is more subject to flotation. Grade patterns for Transects 3 and 4, where prevailing water movements are in the form of alongshore currents, differed considerably from that of Transect 1. Sand to the greater depth at Transect 3 consisted mainly of coarser grades all along the transect. Alongshore flow here was apparently involved in transportation of finer grades toward Transect 4 and North Fishtail Bay (see also Wilson, 1945). Surface sand of Transect 3 was composed almost entirely of finer grades. This layer probably represented sand that was moved on to the transect from farther alongshore. Distribution of finer surface sand may be explained by combined effects of deposition by currents along water line, onshore wave action, and drop in lake level. Accumulation of finer grades in the region of the water's edge at Transect 4 was believed due to diminished velocity of currents that swung toward shore from around the bend. Smaller grains were apparently moved on past more lakeward parts of the transect by stronger flow. Grade pattern of surface sand at time of sampling indicated influences of onshore waves.

Sand at Transects 2 and 5 showed the effect of ridge formation. Lesser percentages of fine grades just before and just past the water line, with increased percentages between, is characteristic of beach ridges. Three ridges, one offshore, were present at Transect 5 at time of sampling.

Under the assumption that grade pattern for the majority of sand grains, i.e., sand to greater depth, will reflect influences of major factors involved, evidence presented here indicates that the greatest selectivity of sand results from washing and subsequent suspension. Flotation plays an important role in water transportation of sand (see Simonds, 1896, Evans 1938a, b, McKelvey, 1941, and Emery, 1945); but since sand moved by this method is mainly from beach surface in the vicinity of the water line, flotation would appear to have little affect upon grade patterns of shoal and upper beach. Although waves of all magnitudes induce surface flotation, sand does not float through breaking waves; and smaller waves or wavelets are responsible for flotation over any great distance. Floating sand is chiefly responsible for swash marks, which indicate heights wave-driven water attains on beaches (Evans, 1938b, Emery, 1945).

Solid Organic Matter

The greater proportion of organic debris present in the psammolittoral zone originates from land and lake vegetation, and its distribution in this zone is mainly dependent upon waves and currents. Some organic matter is autochthonous, but greater quantities are allochthonous. Contributions from land vegetation are made to surface of lake and beach, and that material which remains in the psammon has to be anchored with sand or moved up beyond the limits of wave and current action. Lake contributions of vegetable debris, frequently broken submergent and emergent

plants, are carried shoreward and deposited upon the beach. Unless deposited by maximum waves, such material does not long remain on a beach if it is not incorporated in sand or protected from water transportation by barriers formed of sand. It was difficult to determine by observation the manners in which organic debris is added to sand; and the following account should not be considered exhaustive.

Inclusion of foreign particulate organic matter in the sand is chiefly a near-water-line function, and the presence of large amounts of debris in sand above and below the water's edge often indicates approximate positions of former water lines. Organic debris carried to the shoreline by on-shore waves is evident as a dark, flocculent mass, consisting of terrestrial and aquatic plant and animal material, which extends short distances from shore. In general this material moves in from the bottoms of plant beds or from the shoals, although material floating upon the surface of the lake is also included. Greatest quantities usually occurred where bottoms sloped sharply from shore (Transect 2), but comparable amounts were observed at Transect 5 where shoal sands overlaid considerable debris. Floating accumulations of debris persist for a short time following onshore wave action. They are responsive to almost all water movement; and their fate depends upon direction and intensity of waves, currents, and shoreline processes.

Large quantities of debris are brought to shore by waves of maximum height, but waves of this size do not incorporate organic matter in the sand to any great extent. Some of the material is carried far upshore where parts of it mix with sand that forms swash marks. However, little is covered with sand or permitted to remain on the beach below the swash marks, since no barriers are present to hinder return flow of water down the smooth slope that results from maximum waves. Under these conditions organic debris moves up and down the beach with the water, and parts of it are gradually returned to deeper regions of the lake by undertow.

Moderate and light onshore waves often dispose organic debris in manners that permit it to remain in the psammolittoral region for varying periods of time. Moderate waves are principally involved in the formation of sand ridges at the water line or shortly offshore; and these ridges play an important role in retention of organic debris in the psammolittoral zone. Since ridges have low areas on their landward sides, organic debris accumulated in water before them is regularly washed over into these depressions by water pushed up by waves; and, since the water returns to the lake through the sand of the ridges, the organic material remains in the low areas. Finer grades of sand are carried over the ridges in a similar manner, and in time cover parts or all of the organic debris. Debris is buried on the lakeward sides of ridges by alongshore currents that undercut ridges and permit sand to drop straight out onto the shoal. Material

buried before or behind ridges is frequently washed out again by heavier waves and currents. Offshore bars trap debris between themselves and shore where it is also buried in sand and often left after bars are removed. Bars formed across small bays permit considerable organic debris to be included in the sand that fills the bays behind them (Fig. 4c). On deeper parts of shoals and on bottoms of nearshore plant beds, organic material is covered by sand carried in undertow, but that precipitated from surface currents, and by that dropped from surface flotation. Organic debris incorporated in sand is often washed out again by waves and currents of greater magnitude than those that buried it, and returned to deeper parts of the lake or reincorporated in sand at a new location. Hence, amounts of organic material are not constant either in quantity or location.

The foregoing account, based upon observation, is of necessity limited to larger particles of organic matter which are covered by sand, and which are too large to fit into pore space between sand grains. Interstitial organic particles are microscopic, and barely discernible amounts present in sand near shoreline of Transect 1 denoted that heavy wave action has no greater tendency to add interstitial organic matter to sand than it has to add coarser debris. Amounts present in sand of other transects indicate that this material is usually added to sand by surface deposit, since larger amounts were present in surface sand at greater distances from the water line. Some of this material is produced by psammo-organisms, and such autochthonous debris is subject to washing near the water line. Thus greater amounts of interstitial debris at stations more distant from the water's edge may be said to represent increased deposit of allochthonous and greater retention of autochthonous debris. Organic matter present in sand of upper beach is subject to wind action as is the dry sand of the uppermost layers.

INTERSTITIAL WATER

Water contained in spaces between sand grains forms the habitat of psammo-organisms, and this habitat becomes more restricted when there are lesser amounts of water. Sand of shoal and that of the lower beach has the interstitial volume completely filled with water. Farther upshore more and more air enters the interstices until, near the landward limit of the psammon, water is present only as a film around each sand grain. Amounts of water present in surface layers of beaches are influenced by various physical and meteorological conditions, such as, distance from water line, degree of slope, height of waves, amount of rainfall, relative humidity of the atmosphere, and others. Effects of most of these factors have been brought out in foregoing discussions and will not be repeated here. Capillarity is of importance for regions of beach near the water's edge since more landward parts are too high above water level to be supplied with water in this manner. These latter regions depend mainly upon waves and rain

for their water supply; and quantities of water there are not so constant as amounts in inner beach and shoal sand. For per cent saturation of beaches at various distances from water line see Wiszniewski (1934a) and Pennak (1940).

WATER LINE

Since the water line forms the boundary between the two main divisions of the psammolittoral zone, since transportive agencies have most pronounced effects in its immediate vicinity, and since position with reference to it determines amounts of water present in the beach, it must be regarded as a physical feature of primary importance to psammo-organisms. Variations in position of water line are brought about by rise and fall of lake level and by beach building activities of onshore waves. Fall or rise in water line brings about alterations of Wiszniewski's (1933) three divisions of the psammolittoral zone.

LIGHT

Sassuchin, *et al*, (1927) exposed photographic film at various depths in beach sands of the Oka River and found no light reaction upon film placed at depths of 2 or more cm. The greatest depth at which the light meter used at Douglas Lake recorded the presence of light was approximately 0.5 cm. Differences in methods used here and by the Russian investigators do not permit results to be strictly comparable; but it is evident that light penetrates only the uppermost layers of sand.

CHEMICAL FEATURES

CHEMISTRY OF INTERSTITIAL WATER

Chemical features of water at a depth of 4 cm, which was the depth at which samples were taken, undoubtedly differ from those of water contained in the uppermost layers of sand where most organisms occur. However, it was not possible to withdraw water from surface layers and exclude air or lake water; and on most transects, even at a depth of 4 cm, water could not be withdrawn from sand 50 cm or more above water line except during or shortly after periods of high waves or rainfall. On Transect 6 water could not be sucked from either shoal or beach at any depth that could be reached with the sampling tube. Although its chemical analysis may not furnish data upon features of the strata of more abundant life, water from a depth of 4 cm does offer information concerning processes present and relationships with lake water. Data that are presented in Figure 7 are based upon 10 series of samples made along every transect during the summer of 1942.

Average pH values for the first five transects (Fig. 7) indicate that interstitial water is usually more acid than lake water although water

from sand near shoreline may frequently possess the same hydrogen ion concentration as the lake. Variation at various stations on different transects indicates that spatial relationships with the water line do not always determine pH value. Average hydrogen ion concentration of interstitial

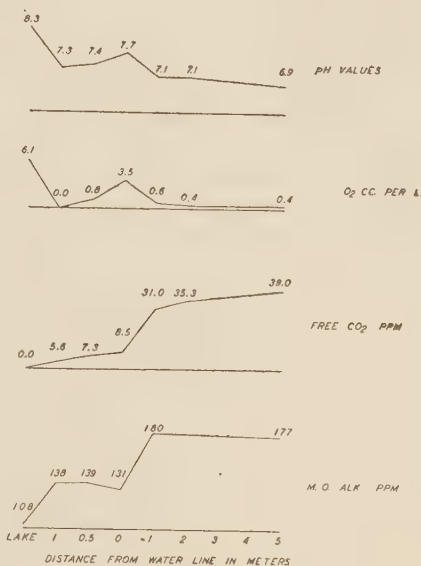


FIG. 7. Averages of four chemical features of interstitial and lake water at Transects 1-5. Lake water is represented at extreme left, and beach sections of transects are to the left of the O stations.

water was lowest at water line and increased both lakeward and shoreward; and shoal stations were usually slightly more acid than beach stations. Wiszniewski (1934a) found interstitial water of Lake Wigry beaches to have the same hydrogen ion concentration as lake water; and, in 1936, he reported interstitial beach water of some Tatras lakes to be more acid than lake water. Stangenberg (1934) gave a pH value of 7.3 for Lake Wigry and pH values of 7.2 and 7.0 for stations 80 cm from water line upon two beaches. Pennak (1940) found that hydrogen ion concentration of interstitial beach water was usually slightly higher than that of lake water.

Average quantities of dissolved oxygen for the first five transects exhibit a curve that is similar to average pH values. Interstitial water always contained less oxygen than did lake water; and amounts present showed an abrupt shoreward and lakeward decrease from water line. Quantities of dissolved oxygen present at any station upon any transect were by no means constant. A similar shoreward gradient has been reported by Wiszniewski (1934a) and Pennak (1940).

Concentration of free carbon dioxide is an extremely variable factor, and average concentrations are not representative of all transects or of any one transect at all times. General horizontal gradients depicted in

the figure often occurred, although more shoreward stations frequently possessed more free CO_2 than did water line stations. Stangenberg (1934) found more free CO_2 in interstitial beach water than in lake water; and Pennak (1940) reported smaller amounts in beach near water line and greater quantities farther shoreward.

Interstitial water did not exhibit phenolphthalein alkalinity; therefore methyl orange alkalinity was due to bicarbonate (half-bound CO_2). Interstitial water always contained more bicarbonate than did lake water, but that present at any one station was not constant either in quantity or in relation to other stations. Large quantities of half-bound CO_2 were usually associated with great amounts of free CO_2 .

SIGNIFICANCE OF CHEMICAL FEATURES

High hydrogen ion concentration, small quantities of oxygen, and large amounts of free CO_2 suggest the presence of organic decomposition in the

TABLE 3. Influence of rain upon chemical features of interstitial beach water at Transect 4

Station	Before rain 7/6/41				After rain 7/7/41			
	pH	O ₂ cc./1	CO ₂ ppm.	MO Alk. ppm.	pH	O ₂ cc./1	CO ₂ ppm.	MO Alk. ppm.
0	7.3	0.4	6.0	124	7.3	0.1	6.0	146
0.5 m.	7.1	0.0	20.0	188	7.3	0.1	9.0	174
1.0 m.	No sample				7.5	0.1	4.0	150
1.5 m.	No sample				7.3	0.1	6.0	148

sand. On parts of beach and shoal where sand stratification is not continually upset by waves and currents, products of organic decay are usually present in greatest concentration. However, spatial relationship to water line does not alone determine the chemistry of interstitial water, since it varies in accordance with forces that affect the shoreline. Also, since, on most transects, it was usually impossible to withdraw water from sand at a distance of 50 cm or more shoreward from water line except after high waves or rainfall, it seems probable that water withdrawn under such conditions represented a dilution with lake or rain water; and samples taken from more landward stations should not be considered representative of usual chemical conditions. Effects of rain upon the chemistry of interstitial beach water are shown in Table 3. Apparently the decrease of free CO_2 was responsible for lower hydrogen ion concentration. Oxygen was added to beach water but quantity at water line was reduced, a circumstance which may have been caused by flow of interstitial water into the lake. Width of sampling area was increased by 1 m. Dilution of interstitial water was indicated by all four chemical features. As shown in Table 4,

waves had much the same influences as did rain except effects were more pronounced near the water line and shoals were affected.

The main influence of waves and rain appears to be dilution or replacement of interstitial water with that of lake or rain. Such dilution is indicated by lower hydrogen ion concentration, greater quantities of oxygen, and smaller amounts of free and half-bound CO_2 . Hence it appears very doubtful that samples from upper beach, which were taken only after waves or rain, represent usual chemical features of water of that region.

Although sand near water line usually contains less interstitial organic debris than is found on more lakeward and shoreward parts of transects, coarser organic matter is frequently present in large quantities; and its decomposition is responsible for large amounts of free CO_2 that are often built up at water line during protracted periods of calm. Wave action

TABLE 4. Influences of wave action upon chemistry of interstitial water of nearshore stations at Transect 1

Station	Average conditions				Following waves			
	pH	O ₂ cc./l	CO ₂ ppm.	MO Alk. ppm.	pH	O ₂ cc./l	CO ₂ ppm.	MO Alk. ppm.
-3 m.	7.0	0.1	13.0	144	7.1	0.5	6.0	120
-1 m.	7.1	1.2	8.0	125	7.5	1.6	5.0	120
0	7.6	4.6	2.5	128	7.8	6.3	1.0	120
0.5 m.	7.7	1.6	1.6	130	8.1	4.7	0.0	142

drives lake water into sand with resultant lowering of free CO_2 ; and small amounts of this gas may represent either recent wave action or small quantities of organic debris. On Transects 4 and 5 low concentrations of carbon dioxide at the water's edge were observed to be due to wave action; whereas lower concentrations at shoreline on Transects 1, 2, and 3 were due to lesser amounts of organic matter in the sand.

Since the largest concentrations of half-bound carbon dioxide were usually associated with the greatest amounts of free carbon dioxide, since samples did not represent surface water, and since the greatest quantities of bicarbonate were found in submerged sand, it does not appear likely that evaporation of interstitial water from the surface of the beach plays the major role in concentration of half-bound CO_2 in sand that other authors (Wiszniewski, 1934a, Pennak, 1940) have given it. It seems more probable that high concentrations of bicarbonate found in sand result from the action of free CO_2 upon calcium carbonate present as marl precipitated from uppermost strata (and upon calcite present in sandstone pebbles in Douglas Lake).

Chemistry of interstitial water is determined by quantities of organic and other materials present in the sand and upon the magnitude of transportive agencies that prevail at any one location. Free and half-bound

CO₂ and hydrogen ion concentration are greater and dissolved oxygen lower in stable sands than in those that are constantly shifted by water movements. Portions of the water pushed upon beaches by wave action return to the lake through the sand. Results of this flow are dilution of interstitial water and transportation of its dissolved materials to the lake. Lake water thus receives free and half-bound CO₂, as well as dissolved organic matter, from the sand. Materials contained in pore space of shoals are added to the lake when the upper layers of sand are moved by water. Products of decomposition of the organic matter that the lake adds to the sand are not entirely lost to the lake. Processes that result in inclusion of organic matter into the sand near water line frequently result in addition to lake water of the materials produced by its partial decomposition farther offshore. Temporary inclusion of particulate organic matter in the sand affords a supply of products of decay to surface lake water when sand covering the material is removed. Products of organic debris originating in psammo-organisms are made available to the lake in a similar manner. However, the firm surface of sand and marl that was formed on the wider shoals did not often permit loss of essential materials to the lake. Since this layer was present on the surface of the greater portion of the psammolittoral zone in Douglas Lake, the lake was unable to draw upon considerable quantities of free and half-bound CO₂ and dissolved organic matter.

CHEMICAL FEATURES OF SAND

Mineralogy

Analysis of Douglas Lake sand by Mr. M. V. Denny disclosed the following minerals:

- quartz (SiO₂) (varieties: chert, flint, jasper, rock crystal, and chalcedony)
- magnetite (Fe₃O₄)
- hematite (Fe₂O₃)
- limonite (Fe₂O₃ · nH₂O)
- feldspar (KAlSi₃O₈) (microcline and orthoclase)
- zircon (ZrSiO₄)
- ilmenite (FeTiO₃)
- chromite (FeCr₂O₄)
- apatite (Ca₅Fe(PO₄)₃)
- calcite (CaCO₃)
- epidote (H Ca Fe Al silicate)
- garnet (Ca Fe Al silicate)
- hornblende (Ca Mg Fe Al silicate)
- tourmaline (H Al B OH silicate)
- chlorite (H Mg Al silicate)
- mica (H K Al silicate)

Sand was composed of grains of rock crystal quartz (approximately 90 per cent), magnetite, zircon, ilmenite, chromite, apatite, calcite, epidote, garnet, and tourmaline. Minerals present in pebbles were: chert, flint, jasper, chalcedony, feldspar, hornblende, chlorite, mica, apatite, calcite (in sandstone pebbles), epidote, and garnet. Magnetite was sometimes present in sufficient quantities to impart a black color to sand; but color due to magnetite should not be confused with the black layer described below. All minerals listed occurred at each transect.

Black Layer

At various depths (usually 5–10 cm) below the surface of the sand there occurred a dark stratum which emitted a foul odor (H_2S) and turned yellow or brown upon exposure to air. The upper limit of this black layer was rather sharply defined, and the stratum varied in thickness (3–10 cm). Black sand of this nature occurred 1.5 cm below the surface at Transect 6, and varied from 2–6 cm below surface on Transects 4 and 5. On the first, second, and third transects its upper limit was 5–10 cm from the surface. Its depth was not uniform along any transect except No. 6.

This black layer has been studied by previous investigators (Ellis, 1925, Danilčenko and Čigirin, 1926, Bruce 1928b, and others) and it seems well established that the black color is due to reduction of iron oxides by sulfides produced by anaerobic decomposition of organic material. Danilčenko and Čigirin stressed reduction of sulfates by bacteria in the presence of organic matter as the main source of sulfides. The only sulfates present in Douglas Lake sand were those that were produced in oxidation of iron sulfide, and these sulfides must result directly from organic decomposition in the absence of oxygen. Upon exposure to oxygen, the iron sulfides are transformed into iron oxides, black color is lost, and free sulfur is released. Interstitial water withdrawn from the black layer was found to contain no oxygen, to have a pH value of 6.6–6.9, and to contain 82–126 and 233–354 ppm free and half-bound CO_2 , respectively.

When dried, sand from the black layer had hematite and limonite coatings upon quartz grains. In order to study some features involved in formation of dark sulfide layers the following experiments were performed: Dry sand from the black layer was placed in a beaker of water through which hydrogen sulfide was slowly bubbled. Within 30 minutes the sand had turned black and the water had a grayish tinge. Some of the sand was removed and divided into three parts. Two portions were placed in evaporation dishes and one dish was kept in the dark. The third portion was placed in a beaker of aerated water. The original beaker with black sand and H_2S saturated water was allowed to stand exposed to atmosphere. Sand contained in the two evaporating dishes and beaker of aerated water regained the yellow-brown color within 30 minutes. Water contained in the original beaker gradually lost its grayish color, its odor of hydrogen sulfide and became

milky. After 10 hours the uppermost 2 mm of black sand turned yellowish brown; and at the end of 4 days the upper 11 mm had reverted to the iron oxide color. Maximum penetration of oxygen as indicated by color change of black sand amounted to 15 mm in 10 days. The water used in the experiments was distilled but was found to have a pH of 6.1 due to contamination by a copper still. After oxidation of sulfides, hydrogen ion concentration dropped to a pH of 6.4. Black sand placed into water with a pH of 6.1 raised pH to 6.4 following oxidation. Evaporation of some of the milky water gave a residue that contained molecular sulfur, but iron was not present in any form. Continued exposure of water containing sulfur resulted in oxidation to sulfate—apparently calcium sulfate.

Color changes associated with penetration of oxygen into black sand indicate that the upper limit of the black layer marks the division between aerobic and anaerobic zones in the sand. However, Bruce (1928b) contends that this is a fallacious impression, since oxygen is known to occur in black sands of marine beaches; and he would prefer to regard the upper limit of the black layer as marking the end-point of one stage of a serial process. He does not object to the viewpoint that the position of the black layer marks a point of equilibrium between sulfide producing reactions of the depths and oxidizing effects of the atmosphere above. Since oxygen was not found in the black layer at Douglas Lake, the demarcation suggested by the upper limit of this stratum may be as clean cut as it appeared. In referring to oxidizing action of the atmosphere, Bruce ignored the effects of photosynthesis in uppermost layers of sand.

The experiments described above indicate that oxygen penetration into sand beneath still water is a process that includes only the uppermost layers (1.5 cm). Iron is not lost to interstitial water in transformation of oxides to sulfides or vice versa, but remains in coatings upon sand grains. Oxidation of sulfides to free sulfur and subsequent transformation of the latter into sulfate tends to alkalize the water medium and perhaps buffers effects of large amounts of free CO_2 .

Variation in depth of black layer is associated with changes in shoreline processes that are involved in transportation of sand and supply of water and organic debris to various regions of the psammolittoral zone. At Transect 6, where no wave action was observed, the upper edge of the black layer closely approached the surface; and its depth there of 1.5 cm was believed to represent penetration of oxygen to a very slight distance past the photosynthetic layer. When water line sand is buried under ridges, depth of black layer is suddenly increased; and a new black layer may be formed that finally incorporates the old layer as sulfide reactions penetrate the sand between. Depth of black layer is consistent upon transects exposed to frequent wave action. Transportation of surface sand is due to agencies that also drive water into sand and this action pushes the black layer deeper as sand is removed. Any actions (waves and rain) that result in addition of

oxygenated water to sand restrict the black layer to greater depth; and periods of calm permit it to build up toward the surface. Degree of dark stratum formation is dependent upon amounts of materials that serve as sources of sulfides, and upon factors that limit sulfide formation. In general the vertical extent of sulfide formation near water line varies inversely with frequency and magnitude of water movements.

BIOLOGICAL FEATURES

LIST OF ORGANISMS STUDIED

Mastigophora, Amoebida, Infusoria, and bacteria were not studied because it was not possible to do accurate work with preserved specimens. Culturing these forms would have consumed too much time; and their study was not considered necessary for purposes of this paper.

PLANTS

ALGAE

Myxophyceae

Chroococcales:

- Merismopedia elegans* A. Braun
- Merismopedia punctata* Meyen
- Merismopedia tenuissima* Lemm.
- Chroococcus turgidus* (Kütz.) Naeg.
- Chroococcus minutus* (Kütz.) Naeg.
- Chroococcus limneticus* Lemm. v. *synechococcus aexuginosus* Naeg.
- Aphanocapsa delicatissima* W. & G. S. West
- Aphanothece* sp.
- Gomphosphaeria* sp.
- Coelosphaerium Naegelianum* Unger
- Coelosphaerium Kuetzingianum* Naeg.
- Microcystis aeruginosa* Kuetz.
- Microcystis incerta* Lemm.
- Microcystis* sp.

Hormogonales:

- Oscillatoria* sp.
- Phormidium* sp.
- Nostoc commune* Vauch.
- Lyngbya Birgei* G. M. Smith
- Anabaena flos-aquae* (Lyng.) Breb.
- Anabaena Bornetiana* Collins
- Cylindrospermum* sp.
- Dichothrix gypsophila* (Keutz) Bor. & Fla.

Heterokontae

Heterococcales:

- Ophiocytium parvulum* (Perty) A. Br.

Bacillarieae

Centrales:

- Melosira ambigua* Müll.*
- Cyclotella bodanica* Eul.*
- Cyclotella Kuetzingiana* Thw.*
- Cyclotella compta* v. *radiosa* Grun. apud V. H.*
- Stephanodiscus astraea* (Ehr.) Grun. apud Cl and Grun.*

Pennales:

- Tabellaria fenestrata* (Lyngb.) Kütz.*
- Tabellaria flocculosa* (Roth) Kütz.*
- Fragilaria brevistriata* Grun. apud V. H.*
- Fragilaria pinnata* Ehr.*
- Fragilaria leptostauron* (Ehr.) Hust*
- Opephora Martyi* Herib.
- Synedra vaucheriae* v. *capitellata* Grun.
- Synedra amphicephala* Kütz.*
- Eunotia arcus* Ehr.
- Eunotia formica* Ehr.
- Cocconeis pediculus* Ehr.
- Cocconeis placentula* v. *euglypta* (Ehr.) Cl.
- Eucocconeis flexella* (Kütz.) Cl.
- Achnanthes lanceolata* (Breb.) Grun. apud Cl. & Grun.
- Achnanthes exigua* Grun. apud Cl. & Grun.
- Mastogloia Smithii* Thw.
- Mastogloia Smithii* v. *amphicephala* Grun.
- Mastogloia Smithii* v. *lacustris* Grun.
- Mastogloia grevillei* W. Sm.
- Mastogloia elliptica* v. *dansei* (Thw.) Grun.
- Caloneis bacillum* (Grun.) Cl.

* Lake plankters found in sand.

- Caloneis alpestris* (Grun.) Cl.
Caloneis silicula v. *truncatula* Grun.
Neidium dubium (Ehr.) Cl.
Neidium dilatatum (Ehr.) Cl.
Neidium iridis (Ehr.) Cl.
Stauroneis anceps Ehr.
Diploneis puella (Schum.) Cl.
Diploneis elliptica (Kütz.) Cl.
Navicula Reinhardtii Grun.
Navicula tuscula (Ehr.) Kütz.
Navicula tuscula v. *minor* (no standing; to be described)
Navicula radiosa Kütz.
Navicula radiosa v. *tenella* (Breb.) Cl.
Navicula lacustris Greg.
Navicula exigua (Greg.) Müll.
Navicula exigua v. *capitata* Patrick
Navicula viridula Kütz.
Navicula bacillum Ehr.
Navicula lanceolata (Ag.) Kütz.
Navicula pupula Kütz.
Navicula pupula v. *capitata* Hust. apud Pasch.
Navicula placentula (Ehr.) Grun.
Navicula oblonga (Kütz.) Kütz.
Navicula peregrina (Ehr.) Kütz.
Navicula vulpina Kütz.
Navicula seminulum Grun.
Navicula pelucida Kütz.
Navicula gastrum (Ehr.) Donklin
Navicula rhynchocephala Kütz.
Navicula scutelloides W. Sm. ex Greg.
Amphipleura pelucida Kütz.
Amphora veneta Kütz.
Amphora ovalis v. *pediculus* (Kütz.) V. H.
Pinnularia viridis (Nitzsch.) Ehr.
Cymbella turgida Greg.
Cymbella affinis Kütz.
Cymbella lanceolata (Ehr.) Kirch.
Cymbella aspera (Ehr.) Herib.
Cymbella cuspidata Kütz.
Cymbella delicatula Kütz.
Cymbella Ehrenbergii Kütz.
Cymbella ventricosa Ag.
Cymbella microcephala Grun. apud V. H.
Cymbella Cesati Grun.
Cymbella parva (W. Sm.) Cl.
Cymbella rupicola Grun.
Cymbella naviculiformis Auersw.
Cymbella cymbiformis Ag.
Cymbella hybrida Grun. ex. Cl.
Cymbella laevis Naeg.
Cymbella hebridea (Greg.) Grun.
Cymbella tumida (Breb.) V. H.
Cymbella sinuata Greg.
Cymbella norvegica Grun.
Cymbella cistula (Hempr.) Kirch.
Cymbella amphicephala Naeg. ex Kütz.
Gomphonema intricatum v. *pumila* Grun. apud V. H.
Gomphonema mustela Ehr.
Gomphonema subtile Ehr.
Gomphonema acuminatum v. *coronata* (Ehr.) Rabenh.
Gomphonema gracile v. *auritum* (A. Br.) Grun. apud V. H.
Cystopleura zebra v. *porcellus* (Kütz.) De-Toni
Cystopleura zebra v. *saxonica* (Kütz.) De-Toni
Cystopleura turgida (Ehr.) Kunze
Cystopleura turgida v. *granulata* (Ehr.) De-Toni
Cystopleura sores (Kütz.) Kunze
Cystopleura argus v. *alpestris* (W. Sm.) De-Toni
Rhopalodia gibba (Ehr.) Müll.
Nitzschia angustata (W. Sm.) Grun.
Hantzschia amphioxys (Ehr.) Grun. apud Cl. & Grun.
Amphiprora ornata Bailey
Cymatopleura solea (Breb.) W. Sm.

The following species were not present in material sent to Dr. Patrick but were identified by the writer.

- Asterionella formosa* Hassal*
Synedra ulna (Nitzsch.) Ehr.*
Diatoma vulgare v. *ovalis* (Fr.) Hust.
Gyrosigma sp.
Stauroneis parvula Grun.

- Stauroneis obtusa* Lagerst.
Stauroneis phoenicentron Ehr.
Navicula pusilla W. Sm.
Navicula cuspidata Kütz.
Pinnularia divergens v. *elliptica* Grun.

* Lake plankters found in sand.

Cymbella angustata (W. Sm.) Cl.
Cymbella austriaca Grun.
Gomphocymbella ancyli (Cl.) Hust.
Cymatopleura elliptica (Breb.) W. Sm.
Surirella elegans Ehr.
Meridion circulare Ag.

Chlorophyceae

Volvocales:

Chlamydomonas sp.
Gonium pectorale Müll.
Pandorina morum Bory

Oedogoniales:

Oedogonium sp.

Chlorococcales:

Scenedesmus arcuatus Lemm.
Scenedesmus bijuga (Turp.) Lag.
Scenedesmus bijuga v. *alternans* (Rein.)
 Borge
Scenedesmus acuminatus (Lagerh.) Chod.
Scenedesmus armatus (Chod.) G. M. Sm.
Scenedesmus dimorphus Kg.
Scenedesmus quadricauda (Turp.) Breb.
Tetradron trigonum (Naeg.) Hansg.
Pediastrum Boryanum (Turp.) Menegh.
Pediastrum Boryanum v. *longicorne*
 Reinsch.

Pediastrum duplex Meyen
Pediastrum intergrum Naeg.
Coelastrum cambricum Arch.
 Zygnematales:
Zygnema sp.
Mougeotia sp.
Spirogyra sp.
Pleurotaenium Ehrenbergii (Breb.) D. By.
Closterium Leibleinii Kütz.
Euastrum gemmatum Breb.
Euastrum sp.
Cosmarium granatum Breb.
Cosmarium Botrylis (Bory) Menegh.
Cosmarium subtumidum Nordst.
Cosmarium sexangulare Lund.
Cosmarium subprotumidum Nordst.
Micrasterias truncata (Corda) Breb.
Xanthidium antilopaeum (Breb.) Kütz.
Staurastrum polymorphum Breb.
Desmidium sp.

Dinophyceae

Dinoflagellatae:

Ceratium hirundinella O. F. M.
Peridinium minutum Kofoid
Gymnodinium sp.

ANIMALS

PROTOZOA

Sarcodina

Rhizopoda

Testacea:

Arcella vulgaris Ehr.
Arcella discoides Ehr.
Arcella dentata Ehr.
Diffugia corona Wallich
Diffugia cratera Leidy
Diffugia pyriformis Perty
Diffugia constricta (Ehr.) Leidy
Diffugia acuminata Ehr.
Diffugia ureolata Carter
Diffugia lobostoma Leidy
Diffugia globula (Ehr.)
Diffugia spiralis Ehr.
Centropyxis aculeata (Ehr.) Stein
Nebela collaris (Ehr.) Leidy
Nebela flabellulum Leidy
Pseudodiffugia gracilis Schlumb.
Quadrula symmetrica (Wallich) Schulze

Euglypha alveolata Duj.
Euglypha ciliata (Ehr.) Leidy
Euglypha cristata Leidy
Euglypha mucronata Leidy
Euglypha brachnata Leidy
Trinema enchelys (Ehr.) Leidy
Hyalosphenia elegans Leidy
Hyalosphenia papilio Leidy
Assulina seminulum (Ehr.) Leidy
Cyphoderia ampulla (Ehr.) Leidy

PLATYHELMINTHES

Turbellaria

Stenostomum sp.

ROTATORIA

Bryceela tenella (Bryce)
Cephalodella spp.
Collothea wiszniewskii Varga (?)
Colurella colurus (Ehr.)
Dicranophorus forcipatus (Müller)

<i>Dicranophorus hercules</i> Wiszniewski trans. ad <i>capucinoides</i>	GASTROTRICHA
<i>Euchlanis arenosa</i> Myers	<i>Gastrotricha</i> spp.
<i>Lecane closterocerca</i> (Schmarda)	Nematoda
<i>Lecane flexilis</i> (Gosse)	<i>Nematoda</i> spp.
<i>Lecane hamata</i> (Stokes)	
<i>Lecane luna</i> (Müller)	TARDIGRADA
<i>Lecane lunaris</i> (Ehr.)	<i>Macrobiotus</i> sp.
<i>Lecane ohioensis</i> (Herrick)	
<i>Lecane mucronata</i> (Harring and Myers)	ANNELIDA
<i>Lecane pomiformis</i> (Edmondson)	
<i>Lecane psammophila</i> (Wiszniewski)	Oligochaeta:
<i>Lecane</i> spp. (5)	<i>Pristina</i> sp.
<i>Lecane crepida</i> Harring ¹	<i>Nais</i> sp.
<i>Lecane nana</i> (Murray) ¹	<i>Naidium</i> sp.
<i>Lepadella patella</i> (Müller)	<i>Ophidonais</i> sp.
<i>Lepadella triptera</i> (Ehr.)	<i>Stylaria</i> sp.
<i>Lindia truncata</i> (Jennings)	<i>Chaetogaster</i> sp.
<i>Mytilina ventralis brevispina</i> (Ehr.)	
<i>Notomata</i> spp. (2)	ARTHROPODA
<i>Scaridium longicaudum</i> Ehr.	Crustacea
<i>Trichocerca iernis</i> (Gosse)	Ostracoda:
<i>Trichocerca insignis</i> (Herrick)	Ostracoda spp.
<i>Trichocerca intermedia</i> (Stenroos)	Copepoda:
<i>Trichocerca insolens</i> (Myers)	<i>Canthocampus</i> sp.
<i>Trichocerca taurocephala</i> (Bauer)	<i>Parastenocaris</i> sp.
<i>Trichocerca tigris</i> (Müller)	<i>Phyllognathus</i> sp.
<i>Trichocerca</i> spp. (5)	
<i>Trichotria</i> sp.	Insecta
<i>Dissotrocha macrostyla</i> Ehr. ²	Coleoptera:
<i>Wierzejskiella velox</i> (?)	Homophronidae larvae
<i>Taphrocampa annulosa</i> Gosse	Diptera:
<i>Proales</i> sp.	Chironomidae larvae
<i>Cephalodella auriculata</i> (Müller)	Ceratopogonidae larvae

¹ Identified by the writer.² Identified by André Burger.

DISTRIBUTION OF ORGANISMS

Vertical Distribution

Sand of Transect 6 was little disturbed by wave and current actions; and, although it was not possible to make many physical or any chemical tests of the environment there, it was assumed that distribution of organisms upon that transect would represent response to habitat infrequently modified by outside factors. As shown in Table 5 organisms were restricted to the uppermost 1 cm of sand. Most evident reasons for such surface concentration were failure of light to penetrate more deeply than 1.5 cm and close relation to surface of the black layer. Sassuchin, *et al*, (1927) have

shown that psammo-organisms, particularly rotifers, are unable to exist in sulfide layers. Observations made during the course of this study corroborate their findings, since, with the exception of certain ciliate protozoans and bacteria, very few organisms were found in black layers. Because chemical features of interstitial water indicate that there is very little mixing with lake water except during periods of water movements, oxygen supply in undisturbed sand probably results mainly from photosynthesis. Concentrations of organisms in surface layers of stable sand indicated their dependence upon photosynthesis for nutrition and oxygen; and the superficial nature of the black layer at Transect 6 did not permit deeper occurrence of strays. Waves and currents usually affected sand near the water line only; and stations in this area of erosion frequently exhibited additions of lake water to interstitial volume of the sand. More lakeward and shoreward stations upon the first five transects generally contained greatest numbers of organisms in upper layers of sand, although restriction to surface strata was often not as well defined as upon the sixth transect. Sulfide layers were not so near surface on Transects 1-5; and smaller numbers of organisms present below depths of 2 cm were regarded as strays from upper layers. Local disturbances brought about alterations of this pattern, but concentration of psammo-organisms in the uppermost 2 cm appeared to be the normal condition in undisturbed sand.

Modifications of Vertical Distribution

Beach Ridges and Sandbars. Actions that resulted in formation of sand ridges also produced concentrations of micro-organisms at depths of 4 or more cm in these structures. Vertical distribution in beach ridges and sandbars is shown in Table 6. A majority of species was present in the deep concentrations, and their position was considered an accumulation brought about by waves that formed the ridges. Since numbers of organisms found in both middle and surface layers of sand ridges were greater than those present in surface layers in the vicinity of such formations, increased numbers at greater depths did not indicate deposit of sand containing fewer organisms atop higher concentrations in surface. Newly formed ridges were often greater than 6 cm. in thickness, therefore original surface layers were not always included in samples. It appeared that numbers of psammo-organisms present in sand ridges were due to transportation of organisms along with sand; and continual deposit of sand with downward flow of water through the uncompacted layers resulted in large numbers of organisms being carried to deeper regions. When not removed by subsequent water movements of different nature, ridges soon exhibited surface concentrations of organisms that were characteristic of undisturbed sand. Organisms in deeper layers moved to surface, encysted in inactive stages, or perished. Some algae (*Pediastrum* and *Merismopedia*) persisted for rather long periods

TABLE 5—Continued

Transect	Station	Depth in cm.	Diatoms	Blue-green algae Chroococcales		Green Algae				Rhizopods			Turbellarians	Rotifers		Gastrottrichs	Nematodes	Tardigrades	Oligochaetes	Ostracods	Copepods	Ceratopogonid larvae
				Merismopedina	Others	Pedastrium	Scenedesmus	Cosmarium	Others	Diffugia Centropyxis	Arcella	Other Testacea		Lecane	Others							
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
3	2 m.	1	2,400	138	110	8	8	37	—	134	45	2	—	3	6	—	—	—	6	—	19	—
	1.5 m.	2	1,100	82	30	5	—	13	2	21	13	—	—	11	28	—	—	2	—	—	5	—
		1	8,000	260	85	6	3	6	—	16	5	—	—	3	2	2	3	—	—	—	6	—
	1 m.	2	5,400	30	34	5	3	—	—	10	—	—	—	3	2	2	—	—	—	—	2	—
		3	1,100	7	19	2	3	2	—	3	—	5	2	10	12	5	3	—	16	—	2	—
	0.5 m.	1	5,700	248	67	8	—	8	2	22	2	—	—	8	2	—	—	—	10	—	2	—
		2	4,000	42	24	2	4	2	—	18	—	2	—	—	3	3	2	—	2	—	2	—
	0.2 m.	3	960	22	14	2	5	2	—	16	—	—	—	—	2	5	—	—	2	—	—	—
		1	10,400	78	53	8	5	2	2	10	—	—	—	8	2	2	—	—	3	—	3	—
	0	2	5,700	90	35	8	5	2	2	14	—	—	—	2	2	3	—	—	2	—	—	—
		3	4,000	22	46	6	2	—	2	10	—	—	—	—	2	3	—	—	—	—	—	—
	-1 m.	4	1,440	40	24	2	13	—	—	5	—	—	—	16	12	2	—	—	—	—	—	—
		1	4,800	51	38	18	—	—	—	10	2	—	—	2	2	2	—	—	—	—	—	—
	-1 m.	2	3,200	56	29	11	7	—	—	11	—	2	—	2	2	3	—	—	—	—	—	—
		3	2,900	59	26	6	3	3	—	18	—	—	—	—	2	2	—	—	—	—	—	—
	-1 m.	4	2,000	26	34	8	3	2	—	8	—	—	—	—	14	10	3	—	—	—	—	—
		1	3,700	51	45	11	8	2	—	3	2	—	2	5	14	2	2	2	6	—	—	—
	-1 m.	2	4,800	100	24	16	5	—	—	14	—	—	—	—	6	2	—	—	—	—	—	—
		3	600	28	18	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	-1 m.	4	1,100	37	30	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		1	5,600	38	38	10	2	—	—	11	2	2	2	5	—	—	—	—	3	—	—	—
	-1 m.	2	4,000	27	19	8	2	3	—	10	—	2	2	—	—	2	—	—	3	—	—	—
		3	1,100	8	5	—	—	—	—	—	—	2	—	—	—	2	—	—	—	—	—	—
		4	—	4	3	2	—	—	—	2	—	—	—	—	—	—	6	—	—	—	—	—

TABLE 5—Continued

Transect	Station	Depth in cm.	Diatoms		Blue-green algae Chroococcales		Green algae				Rhizopods				Rotifers		Gastrotrichs	Nematodes	Tardigrades	Oligochaetes	Ostracods	Copepods	Ceratopogonid larvae
					Merismopedidia	Others	Pediastrum	Scenedesmus	Cosmarium	Others	Diffugia Centropyxis	Arcella	Other Testacea	Lecane	Others	Turbellarians							
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	
	-2	m.	1	35,800	153	441	134	83	26	19	236	—	26	—	6	32	13	—	—	6	—	—	—
			2	3,200	51	198	115	45	6	13	160	—	6	—	—	6	—	—	13	—	—	—	—
			3	2,500	6	122	134	70	—	—	77	—	—	—	—	—	—	—	6	—	—	—	
			4	—	6	38	32	25	—	—	38	—	—	—	—	—	—	—	—	—	—	—	
	-3	m.	1	49,900	166	602	166	128	51	26	179	—	13	—	43	—	90	—	—	—	—	—	
			2	12,000	31	179	134	70	13	6	57	—	26	—	—	—	13	13	—	—	—	—	
			3	3,800	13	115	—	26	—	—	13	—	—	—	—	—	13	—	—	—	—	—	
	-5	m.	1	20,600	269	141	77	51	—	13	25	—	13	—	—	13	—	64	—	—	—	—	
		2	6,400	—	—	13	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
5	5	m.	1	500	156	30	8	2	—	—	208	38	—	2	—	—	10	—	5	—	—	18	
			2	600	14	14	5	2	—	—	24	—	2	3	—	—	—	—	—	5	—	—	8
			3	300	8	11	2	—	—	10	—	—	8	—	—	—	—	—	—	—	—	11	
	3	m.	1	3,700	120	19	5	—	—	333	66	2	2	2	2	—	2	3	10	—	—	37	
			2	1,700	13	16	5	2	—	—	74	2	—	6	—	—	2	5	2	—	—	—	
			3	1,900	10	34	5	—	—	—	40	—	—	2	—	—	—	8	—	—	—	—	
			4	500	8	13	2	—	—	—	16	—	2	3	—	—	—	6	—	—	—	—	
	1	m.	1	4,500	126	37	13	—	—	—	61	22	—	3	8	17	3	6	—	—	—	3	
			2	500	21	13	—	—	—	—	8	2	—	3	—	2	2	24	3	—	—	—	
			3	300	13	11	—	—	—	—	3	—	—	—	—	—	—	27	3	—	—	—	
		4	—	2	8	—	—	—	—	3	—	—	—	—	—	—	—	10	—	—	—		

TABLE 6. Vertical distribution of psammo-organisms in new and old sand ridges as contrasted with that in sand at same stations when no ridges were present. Numerals in body of table designate numbers of organisms per cc. of sand

	Depth in cm.	Diatoms	Blue-green algae (Chroococcales)	Green Algae	Rhizopods (Testacea)	Rotifers	Gastrotichs	Nematodes	Tardigrades	Oligochaetes	Copepods
Average of 10 beach ridges	1	13,900	62	7	27	104	3	0	0	0	0
	2	12,100	8	7	25	14	2	0	0	2	0
	3	56,300	81	12	75	34	0	0	4	14	0
	4	65,200	141	20	126	30	0	3	0	8	0
	5	48,100	173	26	131	5	0	5	3	11	0
	6	24,400	39	8	25	0	0	2	5	5	0
Average of 10 samples at water line when no ridges were present	1	12,600	200	7	18	11	3	8	3	9	0
	2	6,100	26	0	10	0	2	2	2	1	0
	3	1,300	20	3	5	0	0	0	2	0	0
	4	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
Average of 4 sand bars 1 meter offshore	1	25,000	205	63	25	18	0	26	0	13	0
	2	33,200	228	89	51	6	0	26	0	0	0
	3	65,200	447	90	90	0	0	77	0	13	0
	4	2,500	32	0	13	0	0	0	6	0	0
	5	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
Average of 4 samples 1 meter offshore when no sand bars were present	1	17,200	147	242	64	50	0	19	19	6	8
	2	5,600	19	45	6	4	0	10	6	6	0
	3	640	7	13	4	0	2	8	2	0	0
	4	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0
Beach ridge 7 days old	1	10,200	687	3	76	72	2	0	0	2	0
	2	15,500	97	12	131	15	2	2	10	6	0
	3	31,600	104	10	271	0	0	5	3	2	0
	4	5,100	61	13	24	0	0	0	2	0	0
	5	0	65	0	0	0	0	2	0	2	0
	6	0	0	0	0	0	0	0	0	0	0
Beach ridge 10 days old	1	13,260	564	14	176	66	7	16	3	8	0
	2	8,500	103	6	82	0	5	4	47	6	0
	3	5,600	60	3	13	0	2	2	22	3	0
	4	600	8	0	2	0	0	0	16	2	0
	5	0	0	0	0	0	0	0	44	0	0
	6	0	0	0	0	0	0	0	0	0	0

in the vegetative state in deeper strata. Rotifers and some other animals apparently migrated to surface within a few hours after ridges were formed. Organisms buried in sand of ridges were not always compelled to remain until stagnation of interstitial water occurred, since ridges were usually ephemeral in nature. However, during process of removal, or in the event of back-filling, ridges were often unrecognizable; and samples were taken

whose organism count indicated that ridges had been formed shortly before the time of sampling, although they were not evident. Ridges were occasionally left unaltered when their formation was followed by drop of lake level; and in such instances, study of changes in their populations was possible. Ridge formation was the only factor that was observed to result in greater numbers of micro-organisms being driven to deeper layers of sand; and it is believed that deeper concentrations may be attributed to this factor, even though ridges were not evident at time of sampling.

Alongshore Currents. A week alongshore current was once found to result in increased population of deeper sand layers. In this instance, organisms in deeper layers did not outnumber those present in surface. No beach ridge had been formed before this current arose. Alongshore currents usually depopulated sand near the water's edge; thus the concentration due to this one current seemingly represented an unusual condition.

Heavy onshore waves. The result of frequent heavy wave action at Transect 1 was depopulation of sand in areas of erosion. In this area of small populations, organisms were present only in upper layers of sand; and their numbers did not compare to those of surface layers of other transects. Considerable shifting of surface sand is a frequent occurrence on shallows in the region of Transect 1 (see also Moffet, 1943). Since organisms present in the upper 1 cm at Transect 6 usually outnumbered those present to depths of 6 cm on other transects, undisturbed sand appears to present conditions that are most favorable to the development of the majority of species of sand organisms.

Horizontal Distribution

Examination of Table 5 and Figure 8, Transect 6, which presents distribution in sand largely undisturbed, will show that numbers of organisms were rather uniform all along the transect to points of decrease near both ends. Greater numbers present at the water line may have represented more favorable conditions at that station. Otherwise, position with reference to the water's edge appeared to have little effect upon numbers of micro-organisms, except near the two extremities of the transect. Smaller populations near lakeward end were due to deposit of marl and organic debris; and smaller amounts of interstitial water near the landward limit resulted in fewer organisms. No evidences of significant shoreline disturbance were observed at Transect 6, and uniformity of horizontal distribution of organisms in three series of samples did not suggest their occurrence.

Horizontal distribution of micro-organisms along other transects exhibited variations that were associated with shoreline processes. It was not always possible to correlate samples with these actions; therefore causes of all variations were not evident. General features of distribution upon each transect will be briefly discussed and known modifying factors will be included.

Transect 1

Sand was most thickly populated on wider shoals where the firm surface layer was present (Fig. 8); and beach stations exhibited higher concentrations than were found on shallow shoal. Shifting sands that formed the bottom of the area of erosion did not permit development of any considerable sand population.

Transect 2

Largest populations occurred near the lakeward limit of the transect

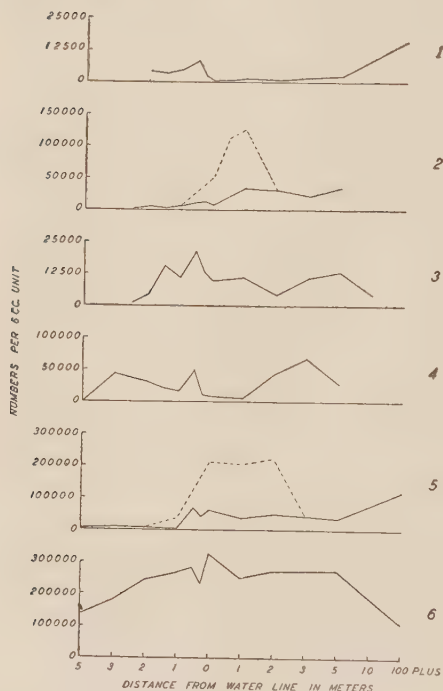


FIG. 8. Horizontal distribution of total sand populations. The 6 cc unit is a core of sand 6 cm deep and 1 sq. cm in cross-sectional area. Transects are numbered in order and landward ends are to the left. Broken lines show influences of sand ridges.

when no sand ridges were present. The area of erosion extended from 1 m above water to 3 m below the water's edge; and in this area most organisms were present at the -1 m stations. Beach populations were similar in number to those of Transect 1. Influences of beach ridges and sandbars upon horizontal distribution are shown by dotted lines in Fig. 8. Alongshore currents depopulated stations near the water line.

Transect 3

Alongshore currents in the vicinity of this transect permitted less development of sand organisms in shallows than upon the beach; and beach populations were somewhat larger than those of Transects 1 and 2. Floccu-

lent bottom deposits were responsible for decrease of numbers of organisms 10 m from shore.

Transect 4

At this transect, the area of erosion extended 2 m into the lake from water line. The most thickly populated sand was found at the - 3 m station which was just below the zone of erosion and just above the area of flocculent marl bottom deposits. Considerable numbers of micro-organisms occurred in the low area of beach 2 - 3.5 m above the water line.

Transect 5

Stations in the immediate vicinity of the water line averaged greater numbers of organisms than did any others in the area of erosion. This sort of distribution indicated the continual formation of sand ridges that were constantly incorporated into smoothly sloping beach by back-filling of their low landward areas. Excepting those present in newly formed ridges (shown by broken lines in Fig. 8) greatest numbers of sand organisms occurred on more lakeward parts of the transect when the firm surface layer of marl and sand was developed.

Undisturbed sand of shallow shoal and lower beach offered the best medium for development of most psammo-organisms. Large concentrations in areas of erosion that resulted from formation of sand ridges did not long persist in the event of removal of ridges or stagnation of their interstitial water. Wave and current action depopulated sand of shallows; and under such conditions more organisms were present in beaches than in shallow shoals if no sandbars had been recently formed. Stability of sand layers appeared to be an essential requirement for maximum development of the majority of sand micro-organisms. In undisturbed sand, the photosynthetic zone is very closely superimposed over the zone of decomposition; and essential compounds produced by chemical and biological processes are not lost from the environment. Firm surface layers developed on deeper shoals serve to protect sand organisms from removal by waves and to retain supply of sulfates, carbonates, dissolved organic matter, and free CO₂. The distribution of organisms in areas of erosion is closely associated with shoreline processes and is not too dependent upon spatial relationships with water line.

Because of frequent disturbances of sand near the water's edge, it was not possible to evaluate the effects of fall in water level except at Transect 6. There no significant decrease in numbers of organisms occurred above water line until surface of sand became dry.

Distribution of Individual Groups

Algae

Diatoms greatly outnumbered all other groups of organisms; and, because of their great abundance, played a major role in the distributional

picture of the total population. Representatives of this group had little tolerance for conditions of stagnation in deeper sand strata and perished within 10 days when left buried in ridges. Horizontal distribution of diatoms closely paralleled that of the total population and there is little need to elaborate upon that feature here.

Blue-green algae, which in numbers ranked next to diatoms, were mainly representatives of the Chroococcales. Filamentous forms (*Nostoc*, *Anabaena*, *Phormidium*, and others) were present but were too few in number to warrant their inclusion in distributional figures and tables. *Nostoc* occurred on the surface of beaches, and its colonies were often broken into separate filaments by waves. Chroococcales were readily separated into the two groups (*Merismopedia*, others) at the magnification used for counting; and the distribution of each group shows positions of concentration that differ in but few respects from those of the total population. *Merismopedia* was apparently able to withstand conditions of stagnation in deeper layers; and its concentrations at depths were often present after diatoms had disappeared. Largest numbers of *Merismopedia* were found in surface layers of sand ridges that had been in existence for several days. Whether larger concentrations under such circumstances represented later additions by waves or increased growth and reproduction is not known; but *Merismopedia* appeared to favor sand in zones of erosion. Representatives of this genus were most abundant upon Transects 3 and 5.

Other Chroococcales (*Chroococcus*, *Microcystis*, *Aphanocapsa*, *Gomphosphaeria*, *Coelosphaerium*, and others) were frequently more numerous than *Merismopedia*, although they did not attain as relatively high numbers near the water's edge or in surface layers of sand ridges. Most representatives of this group were also common lake plankters; and their appearance and numbers in the sand suggested that they were able to adapt to conditions of either environment. The method used to separate debris from organisms in samples from Transect 6 is believed to have included many specimens of this group with the debris.

Green algae were not as common as the blue-greens; and their distribution was not unusual. *Pediastrum* was tolerant of conditions of stagnation in deeper layers of sand ridges.

Testaceous rhizopods (testacea)

This very common group was represented chiefly by *Centropyxis* and *Diffugia*. *Arcella* was present in considerable numbers at distances of 1 m or more upshore from water line; but it did not occur upon Transects 1 and 6 and was not as widely distributed on transects where it was present. Representatives of all three genera were most abundant in upper regions of beaches. Other thecamoebae (*Euglypha*, *Trinema*, *Assulina*, *Nebela*, and others) were less common, and their maximum concentrations occurred in shoal sand. *Diffugia* and *Centropyxis* were concentrated in newly formed

ridges, and their vertical distribution in ridges several days old indicated migration toward the surface. In stable sand testaceous rhizopods were more abundant in the upper 2 cm, but their horizontal distribution was somewhat at variance with that of most other groups. With the exception of greater concentration in upper beach, differences were probably due to variation in reaction to waves and currents.

Rotifera

There was some indication that rotifers favored areas of erosion both above and below water line. However, their horizontal distribution shows that this was not true of all transects. Rotifers were concentrated in sand ridges; but they were able to migrate to the surface and did not remain buried at depths below 2 cm. Wiszniewski and Pennak have stressed the fact that rotifers are more common in sand of beach than in that below the surface of the water. Greater concentration in beach sand was not true of all transects studied at Douglas Lake, where it appeared that the distribution of rotifers in areas of erosion was chiefly dependent upon the nature of shoreline processes, as was the distribution of most other psammo-organisms.

Wiszniewski (1934a) classified sand dwelling rotifers as psammobiotic, psammophilic, and psammoxenic. The first group included those species that occurred only in the sand; the second included rotifers that were able to thrive in the psammon but which were known from other situations; and the psammoxenic group was proposed for rotifers that were not able to survive in the sand. This system of classification has merit, since it is desirable to be able to indicate variation in tolerance to conditions of the psammon; but, since Varga (1938) classed as psammoxenic certain species that were placed in the psammobiotic group by Wiszniewski, there appears to be some question of the validity of all three groups.

Gastrotricha

Gastrotrichs were one of the less common groups, and their distribution in general agreed with that of more abundant forms. They were not included in ridge concentrations and were most numerous within 2 m above and below water line on Transects 2 and 4. They rarely occurred upon the shoal at Transect 1; and on Transect 5 they were most abundant in sand of deeper shoal. Almost without exception, larger numbers of gastrotrichs were present in the upper 2 cm of sand. On Transect 5, where ridges were frequently added to the shoreline, gastrotrichs were absent at the water line.

Nematoda

Small nematodes were very common constituents of the sand populations. They were most abundant on Transects 6, 4, and 2, in that order. Their horizontal distribution was not unusual in any major respects, and they were most common in upper layers of sand.

Tardigrada

Details of tardigrade distribution upon beaches have been given by Pennak (1940). He found their vertical distribution to vary in different beaches and considered their occurrence at depths to indicate their ability to lead a facultative anaerobic existence. He also found horizontal distribution to be sporadic. The distribution of tardigrades upon Douglas Lake beaches and shoals was also sporadic, both horizontally and vertically. On Transect 5, greater numbers occurred on the beach at depths of 3–5 cm. At the –5 m station, larger numbers were present in the upper 1 cm. On Transects 2 and 3, tardigrades were more abundant in shallow shoal where they were mainly confined to surface layers. Their numbers on Transect 4 were larger 1 m shoreward from the water's edge; and they were most plentiful in the upper 2 cm. Tardigrades did not occur upon Transect 1 and were very rare on No. 6. Representatives of this group were not concentrated in sand ridges but they appeared to invade ridges that had been in existence for several days. Since they were found at greater depth in old ridges, they were probably attracted by decomposition of organisms trapped there when the ridges were formed. Although greatest numbers of tardigrades were found at some depth in the beach at Transect 5, their eggs were most abundant in surface layers.

Annelida

Oligochaetes were more numerous in beaches, although they attained almost comparable numbers in shallow shoals of Transects 2, 3, and 5. With few exceptions they were restricted to the uppermost strata of sand, and accumulated in newly formed sand ridges. Many cocoons of various species were present in sand from –3 to 1.5 m stations. Annelids were rarely found on Transect 6.

Copepoda

Of the three genera of copepods found, only one, *Canthocampus*, occurred in sand under water. Concentration of copepods at the –1 m station at Transect 2 was due to representatives of this genus. *Parastenocaris* and *Phyllognathus* occurred only on beaches, where their greatest numbers were attained 2 m or more shoreward from the water line. The latter two genera were very rare on Transects 5 and 6; and beach concentrations of copepods were due to their representatives. Nauplii of all three genera were present. Pennak (1940) found that copepods were most numerous from 1 to 3.5 m above the water's edge. He listed only the genera *Parastenocaris* and *Phyllognathus*. Moore (1939) listed other genera of copepods from submerged sand of the littoral zone but did not include these two. It appears that they occur below water only infrequently if at all.

Insecta

Of the insects found [Chironomidae, Ceratopogonidae (Diptera) and Homophronidae (Coleoptera)], only Ceratopogonidae larvae were studied. Silvey (1936) was chiefly concerned with the Homophronidae and the reader is referred to that paper for details of their life processes. Chironomidae were infrequently observed and little is known of their distribution in the psammon. Eggs and larvae of Ceratopogonidae were common; and details of the distribution of larvae may be gained from Table 5.

Ostracods and turbellarians occurred sporadically in small numbers. For their distribution see Table 5.

OCCURRENCE OF LAKE PLANKTERS IN SAND

Of various lake plankters only diatoms and Chroococcales were commonly found in the psammon. Common plankton diatoms that were present in considerable numbers were: *Asterionella formosa*, *Fragilaria leptostauron*, *Fragilaria brevistriata*, *Synedra ulna*, *Synedra amphicephala*, *Tabellaria fenestrata*, *Tabellaria flocculosa*, *Melosira ambigua*, *Cyclotella bodanica*, *Cyclotella Kutzingiana*, and *Cyclotella compta* v. *radiosa*. The two species of *Tabellaria* were common in sand; but, since sand-dwelling species of *Diatoma* were included with them in counts, they have been excluded from the following discussion. Although common lake plankters, the three species of *Cyclotella* appeared to have psammophilic tendencies, since they were often found alive at distances above water line where other plankton diatoms left only their dead frustules. Since the Chroococcales seemed equally at home in psammon or plankton, it was not possible to determine to what extent they were added either to psammon from plankton or to plankton from psammon.

Diatoms did not form the dominant group of Douglas Lake plankton at the times of collection; and the fact that other plankters were seldom included in a live state in the sand was probably due to differences in specific gravity and powers of locomotion. Some other plankters (*Keratella*, *Cyclops*, *Diaptomus*, and a few cladocerans) were sometimes found stranded on surfaces of beaches behind sand ridges; but, with this exception, they were never found alive in either shoal or beach sand. The following account is based upon living diatoms.

Diatoms discussed in this section are believed to be true plankters. Examination of the same species collected from plankton showed that colonies were larger and more perfect in the lake than they were in the sand; and, with the possible exception of *Cyclotella*, features of their distribution indicated little tolerance for conditions of life in the sand. Even at distances of 50 m or more from shore, where plankton species might be expected to occur upon the surface of the sand, only small broken colonies were present.

Asterionella was often an exception to this rule, since unbroken dead colonies were found at considerable depths in the sand.

Horizontal distribution of lake plankters in the sand is shown in Figure 9. The pattern exhibited by these curves in the vicinity of the water's edge was also characteristic of curves representing horizontal distribution of psammo-organisms when sandbar and beach ridge populations were excluded. This similarity suggests that concentrations of sand micro-organisms in sand just above water line are due to their suspension in water moving toward the shore. Plankton species apparently were added to the sand just above water by waves breaking upon shore; and concentrations of psammo-organisms at the same places probably represented their transfer to this region from sand of the adjacent shoal. Additional evidence that supports this idea will be presented later. Plankton diatoms were not concentrated with psammo-organisms in sand ridges and, in areas of erosion, their numbers were always greater just above water line. Variation in distance above water line at which plankters disappeared was due to differences in height attained by wave-driven water and to differences in slope of beach. Greater numbers of plankton diatoms on deeper shoal surfaces resulted from deposit onto sand where there were lesser movements of water. Smaller numbers of plankters on sand in shallows were due to lesser deposit and more frequent water movements.

Greater concentrations of lake plankters were found in the uppermost 2 cm of sand; but frequently greater numbers occurred in the second rather than in the first centimeter. Large numbers of empty frustules were sometimes observed in samples from greater depths, to which diatoms were probably driven by water flowing toward the lake through the sand. On wide shoals at distances of 50 m or more from shore, they were more abundant in the upper 1 cm.

OCCURRENCE OF PSAMMO-ORGANISMS IN LAKE PLANKTON

Representatives of all major groups of sand micro-organisms were found in plankton samples taken above the transects. Studies of psammo-organisms in plankton were complicated by the fact that certain representatives (*Diffugia globula*, Chroococcales, and *Pediastrum*) were able to live as either plankters or psammo-organisms; and, for reasons of accuracy, they were not included with sand organisms in plankton counts. These groups were more numerous per unit volume in the sand than they were in the lake; but large numbers of them often occurred in the plankton when other groups from the psammon were not present.

Plankton samples taken in onshore and offshore currents at Transect 5 (Fig. 10a) indicate that most psammo-organisms are brought into suspension from the shallow shoal. The landward current contained no sand dwellers until it came within 20 m of shore; and the greater number of the organisms it contained 2 m from shore came from sand within 5 m of the water

line. Water moving lakeward contained most sand organisms 2 m from land and lost most of them before it flowed out 5 m. Greater numbers present at all distances in the offshore current were likely due to washing of the sand at the water line as the incoming current turned alongshore. Many of the psammo-organisms present in the onshore current were probably added to

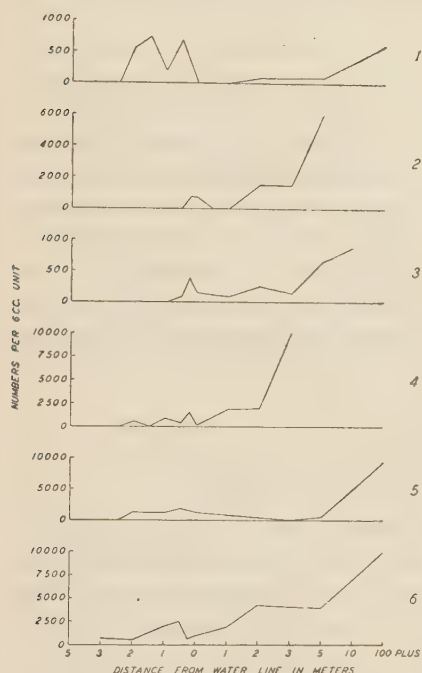


FIG. 9. Distribution of lake plankton diatoms in sand. Landward ends of transects are to the left.

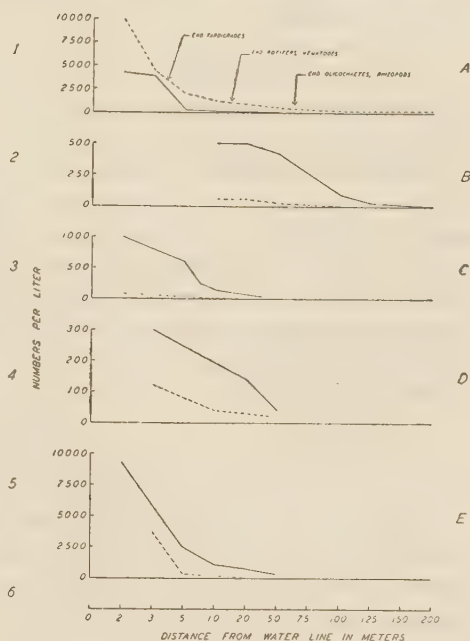


FIG. 10. Occurrence of psammo-organisms in plankton. A. Numbers of sand organisms in plankton in paths of onshore (solid line) and offshore (broken line) currents at Transect 5. B. Transect 1. Solid line,

alongshore waves; broken line onshore waves. C. Transect 2. D. Transect 3. E. Transect 4. In the latter three figures, solid lines indicate periods of alongshore current and broken lines times of onshore waves.

the sand above the water's edge. The offshore current did not add to its numbers of psammo-organisms as it flowed over the shallow shoal. Very few sand organisms were carried any great distance in this stream, and distances at which various groups disappeared from the water arc indicated on the curve. It should be evident from the figure that some regions of shallows receive organisms from other regions. Plankton studies in the regions of the first four transects (Figs. 10 b, c, d, e) indicated that alongshore waves and currents were more effective than onshore waves in washing organisms from the sand. Very few psammo-organisms were present in water during periods of calm.

Similarities in the distribution of both psammo-organisms and plankters in sand near the water line appear to be due to the fact that both groups are in suspension in water moving toward the shoreline. The fact that plankton diatoms were not found concentrated in sand ridges may suggest that concentrations of psammo-organisms in such structures are brought about by some other means.

The depopulation of shallow shoal results in additions of psammo-organisms to the region of the lower beach and to other parts of submerged sand. Very few organisms are added to the lake: and plankton samples taken at depths of 5-7 m 100 m offshore indicate that there is continued settling of the relatively few sand organisms that are moved farther out into the lake.

The extent to which psammo-organisms were moved and returned to sand under onshore, alongshore, and offshore currents at Transect 5 was indicated by counts of organisms from sand under the currents. Under the onshore current, 5 m offshore, sand contained 23,000 organisms per cc; sand under the alongshore current, 0.5 m from shore, had only 14,000 organisms per cc; and sand 5 m from shore under the lakeward current possessed 45,000 organisms per cc.

DISCUSSION

NATURE OF THE PSAMMOLITTORAL ENVIRONMENT

All organisms studied in this investigation appeared to be restricted to the uppermost layers in undisturbed sand. Such surface concentrations resulted from shallow penetration of light and from the apparent toxicity of chemical features associated with organic decomposition and sulfide formation in deeper layers. Algae were dependent upon light for photosynthesis; and most other organisms were supplied with food and oxygen in the photosynthetic zone. Oxygen penetration into sand (based upon experiments) from lake water and the atmosphere was apparently a process that affected the top 1.5 cm. The upper boundary of the black sulfide layer appeared to mark the depth to which conditions were tolerable for most micro-organisms.

Large quantities of autochthonous and allochthonous interstitial organic debris, and the close relationship of zones of photosynthesis and decomposition appeared to be major factors in the high biological productivity of stable sand. On wider shoals, where sand was little disturbed by water movements, psammo-algae enhanced the physical stability of their environment by deposit of marl which bound together grains of sand in surface layers.

Sand in zones of frequent water movement offered environmental conditions that varied in accord with waves, currents, and shoreline processes. Some results of movements of sand were not detrimental to all psammo-organisms, but frequent strong water movements either greatly depopulated the sand or resulted in conditions in which micro-organisms were unable to become well established. In zones of erosion, the only population con-

centrations that were comparable to those developed in stable sand resulted from the formation of sand ridges; and, since the greater number of sand organisms were driven to deeper layers of ridges, such concentrations were temporary in nature. Unless buried under 3 or more cm. of sand, most species of micro-organisms were evidently able to contend with a shifting environment. However, the ephemeral nature of their residence in any one location usually offered psammo-organisms little opportunity to add to their numbers by reproduction.

It has been pointed out that forces which brought about movements of sand on beach and shoal near water line were also responsible for the distribution of organisms in that region. Frequently, the distribution of psammo-organisms in areas of erosion indicated the nature of the most recent shoreline processes. On Transect 6, where little water movement occurred, numbers of organisms in sand under shallow water were approximately equal to those in sand of lower beach. On Transects 1, 3, and 4, where shallow shoal sand was frequently shifted, the beach offered more opportunity for development of micro-organisms. Position of greatest population concentrations in the water line region of Transects 2 and 5 varied below and above the water's edge. Gentle to moderate onshore waves that did not form ridges resulted in concentration of organisms in sand just above the water line; and many groups that were so concentrated were washed from the bottom under shallow water. Alongshore wave and current action resulted in depopulation of both shallow shoal and lower beach, but effects were more pronounced in the former.

Some micro-organisms (copepods of the genera *Parastenocaris* and *Phyllognathus*) occurred only in upper beaches; others (testaceous rhizopods) often attained maximum development in upper eupsammon; and still others (rotifers and gastrotrichs) appeared to favor the area of shifting sand on shallows and beach near the water line. Some species (tardigrades) appeared to be attracted by decomposition of psammo-organisms in deeper layers of ridges. However, the majority of species composing the population attained greater development in the surface layers of stable sand of shoal or lower beach. If greater numbers of micro-organisms indicate a more suitable environment, regions of the Douglas Lake psammolittoral zone in order of more favorable conditions are: 1, stable sands in shallow shoals and lower beaches; 2, areas of deeper shoal where a firm marl surface is developed; and 3, the region of shifting sands above and below water line.

RELATIONSHIPS WITH THE LAKE

Much of the organic material in the sand owes its origin to the lake. Large quantities of coarse organic debris are incorporated in the sand in the vicinity of the water line by certain wave actions; and interstitial particles are added to shoal sands by sedimentation from the lake. The decomposition of this material in the sand produces considerable quantities of dissolved

organic matter and free CO_2 . Action of the latter upon marl precipitated by psammo-algae and upon calcite contained in sandstone pebbles results in large amounts of bicarbonate. Since there is a very close relationship between zones of photosynthesis and decomposition, materials produced directly and indirectly by decay of organic matter become readily available to psammo-organisms. The lake also adds to the sand certain representatives of its plankton whose death augments quantities of materials important to productivity. In zones of shifting sand near water line, products of organic decomposition become available to the lake when there is washing of sand layers containing these materials. Much larger areas of sand are protected from erosion by a firm surface layer that has been described. Except in the infrequent instances when this layer is broken, the lake cannot draw upon products of the decomposition of its own organisms in the greater part of shoal sand. In water line regions, some psammo-organisms enter the plankton; but most of them quickly settle again to the sand. Unless the sand is moved by waves or currents very little mixing of interstitial and lake water occurs on shoals; and materials present in the former are not given up to the latter. Beach interstitial water is added to the lake when wave-driven water returns down through the sand and when rain flows down the strand.

Since many plankters and considerable quantities of organic matter settle to surface of sand on deeper shoals and remain, there does not appear to be sufficient washing of deeper shoal (1.5–2 m) to result in very frequent or intense molar action. Thus it seems that the lake places considerable amounts of the products of its own biology in a situation from which relatively small quantities can be recalled. Inclusion of organic debris in sand prevents its being carried to the profundal region, where, during summer stagnation, it would not exert much influence upon lake productivity. The lake benefits to some extent from products of organic decay that are washed from sand in erosion zones; and it may be contended that the lake obtains in this manner materials that would otherwise be unavailable to it before the overturn. However, in exchange of materials and organisms between the lake and the psammon the balance is in favor of the latter. Therefore it seems fairly safe to assume that great development of the psammolittoral population has in general an adverse effect upon lake productivity. Plankters of such nature as permits their incorporation in the sand, and various agencies that include them and organic debris, rob the lake of material that would add to the productivity of its water.

SUMMARY

1. Augmentation and depletion of organic matter in sand, changes in chemistry of interstitial water due to dilution with lake water, transportation of sand organisms, addition of psammo-organisms to plankton, concentration of sand organisms in ridges, addition of lake plankters to sand

above water line, interference with development of psammolittoral populations, and additions to lake water of materials contained in sand are all influences of waves and currents upon the psammon.

2. The upper limit of the black sulfide layer appears to mark the boundary between aerobic and anaerobic zones in the sand.

3. Organisms present in Douglas Lake psammon in order of preponderance are: diatoms, blue-green algae (Chroococcales), testaceous rhizopods, green algae, nematodes, rotifers, oligochaetes, tardigrades, copepods, gastrotrichs, flatworms, insect larvae (Diptera and Coleoptera), and ostracods.

4. In undisturbed sand, most psammo-organisms are able to exist only in the uppermost layers.

5. The greatest development of the sand population occurs in stable sand of shallow shoal or lower beach.

6. High biological productivity in undisturbed sand is apparently due to the close relation of the photosynthetic and decomposition zones.

7. Distribution of sand organisms in zones of erosion is chiefly dependent upon the nature of shoreline processes.

8. Great development of psammon populations appears to have an adverse effect upon the biological productivity of lake water.

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